UNIVERSITY *of* TASMANIA

The spatial, temporal and structural distribution of Antarctic seafloor biodiversity

by

Jan Jansen, Dipl.-Biol.

Under the supervision of
Craig R. Johnson
Nicole A. Hill
Piers K. Dunstan
and **John McKinlay**

Submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy
in Quantitative Antarctic Science

Institute for Marine and Antarctic Studies (IMAS), University of Tasmania

May 2019

In loving memory of my dad,
whose passion for adventure, sport and all of nature's life and diversity
inspired so many kids, including me,
whose positive and generous attitude touched so many people's lives,
and whose love for the ocean has carried over to me.

The spatial, temporal and structural distribution of Antarctic seafloor biodiversity

by Jan Jansen

Abstract

Biodiversity is nature's most valuable resource. The Southern Ocean contains significant levels of marine biodiversity as a result of its isolated history and a combination of exceptional environmental conditions. However, little is known about the spatial and temporal distribution of biodiversity on the Antarctic continental shelf, hindering informed marine spatial planning, policy development underpinning regulation of human activity, and predicting the response of Antarctic marine ecosystems to environmental change. In this thesis, I provide detailed insight into the spatial and temporal distribution of Antarctic benthic macrofaunal and demersal fish biodiversity. Using data from the George V shelf region in East Antarctica, I address some of the main issues currently hindering understanding of the functioning of the Antarctic ecosystem and the distribution of biodiversity at the seafloor. The focus is on spatial biodiversity prediction with particular consideration given to previously unavailable environmental factors that are integral in determining where species are able to live, and the poor relationships often found between species distributions and other environmental factors.

Food is a fundamental requirement of life, influencing the distribution of all animal species, and for species living at the seafloor below the photosynthesis zone, this food derives from surface primary production. In **Chapter 2**, I present an interdisciplinary approach for modelling the redistribution of food-particles from the ocean-surface to the seafloor, combining satellite-data with an ocean-model, particle tracking, and diatom abundances from sediment grabs for validation. I show that different aspects of the estimated seafloor food-availability link directly to the abundance and richness of key Antarctic seafloor macrofauna observed from camera still-images. I then combine observations from the seafloor, bathymetry, and food-availability estimates to produce a (validated) predictive map of the distribution of important habitat-forming suspension feeders on the George V shelf (**Chapter 3**). Using a similar approach, in this chapter I also predict strong responses in the abundance of suspension feeders to changes at the ocean surface caused by a major glacier calving event in 2010.

Biodiversity has many different attributes. Aside from the abundance of habitat-forming fauna, which is an important proxy for biodiversity, the spatial distribution of single species is also important in determining community structure. However, many species are rare which is why researchers have historically grouped species together based on taxonomic or functional similarity before modelling. Joint-species distribution models can aggregate species based on similarity in their responses to environmental factors, allowing prediction of the spatial distribution of multiple species, including rare species, with higher confidence than other more commonly used statistical methods, and with fewer assumptions regarding associations between grouped species. I use joint-species distribution models

for mapping the distribution of diversity and community structure in benthic macro-invertebrates (**Chapter 4**) and demersal fish (**Chapter 5**). In chapter 4, I also analyse species-level data of benthic macro-invertebrates that are *a-priori* aggregated into higher level taxonomic and functional groups of species, and show that aggregating species into higher level groupings leads to increased model-uncertainty (**Chapter 4**).

Comparing patterns in the spatial distribution of demersal fish and benthic invertebrates, I then show that communities of benthic species can be described along four broad habitat types characterised mainly by depth and slope of the seafloor, *namely* shallow-flat, shallow-steep, deep-flat, and deep-steep environments, with food-availability additionally influencing these habitat distinctions (**Chapter 5**). In this chapter I conceptualise knowledge about community structure and interactions among functional groups and key environmental drivers in the Antarctic benthic ecosystem in a qualitative network topology, test how differences in the environmental setting affect ecological structure, and validate the dynamic network model results with the mapped distributions of fish and macro-invertebrates, revealing insight into ecosystem functioning. This work shows that the large scale spatial, temporal and structural distribution of Antarctic benthic biodiversity is mainly influenced by depth and slope of the seafloor and by the availability of surface-derived food, which links the seafloor strongly to environmental processes at the ocean-surface. Inclusion of the food-availability models results in more accurate mapping of the spatial and temporal distribution of Antarctic marine biodiversity. The high confidence in the spatial predictions of benthic biota means that the representativeness of future Marine Protected Areas can be better assessed and possible changes in the benthic ecosystem due to environmental or human pressures can be better detected and understood. Future predicted increases in primary production will likely result in higher abundances of benthic suspension feeders and alter community composition, but patterns are variable, even within regions.

The advances presented in this thesis can form the basis for future work to map the distribution of Antarctic benthic biodiversity on a circumpolar scale, identify habitats and species assemblages critical for conservation, quantify the total biomass of Antarctic benthic communities, estimate the contribution of Antarctic benthic communities to the sequestration of atmospheric carbon, and estimate how these communities will change in the future based on climate projections.

In **Chapter 6**, I review and discuss how technological and collaborative advances, including those outlined in this thesis, allow us to predict marine biodiversity unlike ever before. The spatial and temporal scales at which predictions are now possible, and the confidence in the predictions themselves, help us to better assess management and policy decisions from local to global scales. These recent developments also allow exploring new ways to predict biodiversity in the future, for the mutual benefit of marine ecosystems and humanity.

Statements and declarations

Declaration of originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

Authority of access and statement regarding published work contained in the thesis

The publishers of the papers comprising Chapters 2 to 6 hold the copyright for that content, and access to the material should be sought from the respective journals. The remaining non-published content of the thesis may be made available for loan and limited copying and communication in accordance with the Copyright Act 1968.

Signed:

Jan Jansen

PhD candidate
Institute for Marine and Antarctic Studies (IMAS)
University of Tasmania

Date: 21/11/2018

Statement of co-authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Jan Jansen (**JJ**), Institute for Marine and Antarctic Studies
Craig R. Johnson (**CJ**), primary supervisor, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia
Nicole A. Hill (**NH**), supervisor, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia
Piers K. Dunstan (**PD**), supervisor, CSIRO Oceans and Atmosphere, Hobart, Australia
John McKinlay (**JM**), supervisor, Australian Antarctic Division, Kingston, Australia
Leanne K. Armand (**LA**), Australian National University, Canberra Australia
Romain Causse (**RC**), Muséum National d'Histoire Naturelle, Paris France
Eva A. Cougnon (**EC**), Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia
Marc P. Eléaume (**ME**), Muséum National d'Histoire Naturelle, Paris France
Scott D. Foster (**SF**), CSIRO Data 61, Hobart, Australia
Benjamin K. Galton-Fenzi (**BG-F**), Antarctic Climate & Ecosystem Cooperative Research Centre, University of Tasmania, Hobart, Australia; Australian Antarctic Division, Kingston, Australia
Philippe Koubbi (**PK**), Sorbonne Université, Paris, France
Alexandra L. Post (**AP**), Geoscience Australia, Canberra, Australia
Michael D. Sumner (**MS**), Antarctic Climate & Ecosystem Cooperative Research Centre, University of Tasmania, Hobart, Australia; Australian Antarctic Division, Kingston, Australia
Jessica Melbourne-Thomas (**JM-T**), Antarctic Climate & Ecosystem Cooperative Research Centre, University of Tasmania, Hobart, Australia; Australian Antarctic Division, Kingston, Australia
Jonathan P. Warnock (**JW**), University of Pennsylvania, Philadelphia, USA
Skipton N. C. Woolley (**SW**), CSIRO, Hobart, Australia

Author details and their roles:

Chapters 2, 3, 4, 5 and 6 of the thesis have been prepared as manuscripts for submission to peer-reviewed journals. In all cases, the concept and design of the research, data analysis, interpretation of results, and the preparation of the manuscripts were the responsibility of the candidate but were carried out in consultation with specialist contributors. The contributions are highlighted for each chapter below.

Chapter 2 - Abundance and richness of key Antarctic seafloor fauna correlates with modelled food-availability

JJ was the primary author and drafted the majority of the manuscript. **JJ** contributed approximately 70% to the planning execution and preparation of the work for the paper, including the study design, software development, data analysis and the preparation of illustrations.

NH and **CJ** contributed significantly to conceiving and designing the study, contributed to data analysis and drafting the paper. **PD** contributed to designing the study, the data analysis and revised the paper. **JM** contributed to developing the software, analysis the data and revised the paper. **MS** contributed to developing the software and revised the paper. **AP** contributed to conceiving and designing the study and revised the paper. **BG-F** contributed to designing the study and writing the paper. **LA**, **ME** and **JW** contributed data, and critically revised the paper.

Chapter 3 - Mapping Antarctic suspension feeder abundances and seafloor food-availability, and modelling their change after a major glacier calving

JJ was the primary author and drafted the majority of the manuscript. **JJ** contributed approximately 80% to the planning execution and preparation of the work for the paper, including conceiving and designing the study, data analysis and the preparation of illustrations.

NH contributed significantly to conceiving and designing the study, contributed to data analysis and drafting and writing the paper. **PD** contributed to designing the study, the data analysis, and drafting and revising the paper. **EC** contributed to designing the study and revising the paper. **BG-F** contributed to revising the paper. **CJ** contributed to designing the study, data analysis and drafting and revising the paper.

Chapter 4 - Taxonomic resolution, functional traits, and the influence of species groupings on mapping Antarctic seafloor biodiversity

JJ was the primary author and drafted the majority of the manuscript. **JJ** contributed approximately 80% to the planning execution and preparation of the work for the paper, including conceiving and designing the study, data analysis and the preparation of illustrations.

NH, **PD** and **CJ** contributed to conceiving and designing the study, contributed to data analysis and drafting and revising the paper. **ME** contributed to data analysis and revising the paper.

Chapter 5 - Combined assessment of the spatial distribution and structural dynamics of deep benthic Antarctic marine communities

JJ was the primary author and drafted the majority of the manuscript. **JJ** contributed approximately 80% to the planning execution and preparation of the work for the paper, including conceiving and designing the study, data analysis and the preparation of illustrations.

NH, **PD** and **CJ** contributed to conceiving and designing the study, contributed to data analysis and drafting and revising the paper. **JM-T** contributed to data analysis and revising the paper. **RC** and **PK** contributed data, and contributed to data analysis and revising the paper.

Chapter 6 – Predicting marine biodiversity

JJ was the primary author and drafted the majority of the manuscript. **JJ** contributed approximately 80% to the planning execution and preparation of the work for the paper, including conceiving and designing the study, and the preparation of illustrations.

NH, **PD, SF, SW** and **CJ** contributed to conceiving and designing the study, drafting the structure of the paper and revising the paper.

We the undersigned agree with the above stated proportion of work undertaken for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed:

Prof. Craig R. Johnson

Supervisor
Institute for Marine and Antarctic Studies (IMAS)
University of Tasmania

Date: 21 Nov 2018

Signed:

Dr. Delphine Lannuzel

Deputy Head of Centre for Oceans and Cryosphere
Institute for Marine and Antarctic Studies (IMAS)
University of Tasmania

Date: 21/11/2018

Acknowledgements

Writing this thesis would not have been possible without the support of a great number of people, including my supervisors, colleagues, friends and family.

To Craig, thank you for being so welcoming from the very first time we met back in 2013. Although I was quickly dismissed from our first encounter with the words ‘I don’t have time today’, the enthusiasm and welcoming spirit you’ve shown during our meeting the following day was one of the main reasons I decided to start my PhD in Tasmania. Thank you for pushing the right buttons when at first the scholarship didn’t come through, and for successfully guiding me through the PhD. Thank you for your advice, for your critical thinking and for writing the ARC-grant with me. Thank you for sharing a very memorable time with me and my dad on board of your yacht and thank you for your support in difficult times.

To Nicole, I really cannot thank you enough for being a pillar of support throughout the last four years. Be it the countless meetings, the numerous reviews of my manuscripts or accommodating me in Kuala Lumpur, these were all vital in enabling me to finish the PhD. Thank you for your friendship and also thank you for helping me find work after my PhD.

To Piers and John, thank you for your sound statistical advice and for the many meetings that greatly helped me navigating through my PhD.

Thank you to all the co-authors of the individual thesis chapters for their support, data, critical reviews, comments, guidance and helpful insights.

Over the course of my PhD, I have also received a lot of support from colleagues that did not co-author any of my thesis-chapters. Of those colleagues, a special thank you goes to Ben Raymond and Simon Wotherspoon who supported me particularly during the early stages of my candidature.

Throughout my PhD, I was supported by a Tasmanian Graduate Research Scholarship and by a generous QAS Top-Up scholarship.

To all my friends and family, thank you for your support, for a lot of fun and for ensuring I’ve got a healthy work-life balance most of the time with plenty of volleyball, surfing, travels and socialising. Keep it up ☺.

To Bine, thank you for travelling with me to Australia and Tasmania in the first place, thank you for your support and listening to thousands of practice rounds of oral presentations, and of course thank you for all the adventures we shared, and for those that are still to come.

Table of Contents

List of Figures

List of Tables

Chapter 1

Introduction

Thesis background / rationale for research

Biodiversity is nature's most valuable resource (Tilman et al. 2014). It is a key element of ecosystem function and stability, has an immense, indirect economic value providing pharmaceuticals and food security, maintaining water quality and facilitating the oceans capacity to recover from perturbations (Worm et al. 2006), and has significant social and cultural value. The Southern Ocean contains significant levels of biodiversity, due to a combination of exceptional environmental conditions and its isolated history (Clarke et al. 2004, Gutt et al. 2004, Brandt et al. 2007). For example, 42-56% of benthic marine species and up to 97 % of species within certain groups (De Broyer et al. 2014, Chown et al. 2015), are thought to be endemic to the Southern Ocean (Griffiths et al. 2009), highlighting the important contribution of this region to global marine biodiversity.

This unique biodiversity is subject to increasing human pressure through economic interest (Kock 2007, Welsford et al. 2014) and the rapid rate of environmental change (Walther et al. 2002, Orr et al. 2005, Hoegh-Guldberg and Bruno 2010a). The importance of Southern Ocean ecosystems and the need to manage pressures on them has been recognised by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) through the creation of a plan to set up a representative system of marine protected areas (MPAs) (CCAMLR 2011). The move to establish MPAs has created demand to acquire comprehensive knowledge of the spatial distribution of biodiversity and its environmental drivers. This knowledge can also form a baseline and may be able to inform future monitoring initiatives.

However, collecting comprehensive biological data is particularly difficult, time consuming and expensive in the Southern Ocean, largely due to its size, remoteness and the extreme nature of the environment. Consequently, biological data are patchy and sparse (Brandt et al. 2007, Griffiths 2010, Gutt et al. 2013a). One way that the gap in knowledge of spatial patterns of biodiversity has been addressed is through bioregionalisation (e.g. Grant et al. 2006, Sharp et al. 2010, Raymond 2011, Douglass et al. 2014). Bioregionalisations aim to spatially subdivide areas in a way so that each subdivision contains a homogenous environment relative to adjacent regions (Douglass et al. 2014), and typically include environmental variables that have been found to generally influence the relevant fauna, such as bathymetry, surface production and temperature (e.g. Raymond 2011, Douglass et al. 2014). These environmental habitats are assumed to be surrogates for biological assemblages. However, because biological variables are typically not included in the classification, unless the bioregionalisation has been validated indirectly by testing the models against direct observations, it is not possible to predict whether biotic assemblages actually differ between (or within) bioregions. Further the shape of the relationship between environmental variables and the biological assemblages is unknown, meaning differences between areas might be exaggerated or understated depending on the shape of the relationship. Determining regions based on community or species' occurrence in conjunction with environmental variables, often termed 'ecoregionalisation', is a more robust alternative approach (Bax 2011) that has been successfully demonstrated for demersal fish on George V shelf in East Antarctica (Koubbi et al. 2010). Quantifying relationships between remotely sensed or modelled data that have broad spatial coverage and spatial patterns of biodiversity is an efficient way to maximise the use of sparse biological data. In addition, this kind of model can be used to predict the biodiversity with a

quantifiable level of uncertainty in unsampled areas where only information about relevant environmental variables is available, thus increasing knowledge in areas where biological sampling is particularly difficult.

Species communities at the seafloor are the most biodiverse component of the marine ecosystem (Angel 1993), including in the Antarctic, where the number of macrozoobenthic species alone is conservatively estimated to be more than 17,000 (Gutt et al. 2004). The species communities living at and near the Antarctic seafloor are not only diverse, they also play an important role in the functioning of the Antarctic marine ecosystem, such as in the food-web (e.g. as feeding-grounds for iconic Antarctic marine fauna such as penguins and seals (e.g. McConnell et al. 1992, Tremblay and Cherel 2000, Takahashi et al. 2003)), and play a role in the global biogeochemical cycle by sequestering carbon (Barnes and Sands 2017). Understanding how these unique communities are distributed on the continental shelf and how they respond to environmental changes is critical for managing and conserving the functioning of the entire Antarctic marine ecosystem.

However, although Southern Ocean benthic communities have been the subject of investigations since the 1950s (Gutt et al. 2013c), still relatively little is known about the spatial distribution of benthic biodiversity on the continental shelf (Gutt et al. 2013c). The rarity of many Antarctic species and inconsistent relationships between biological data and environmental conditions across the regions and taxa studied (Cummings et al. 2010, Convey et al. 2014) are the main reasons that the distributional patterns of seafloor biodiversity around Antarctica remain relatively poorly understood (Brandt et al. 2007, Chown et al. 2015). Importantly, information about relevant environmental variables influencing seafloor communities is missing. The availability of food at the seafloor, which influences the distribution of all benthic animal species, is only approximated through the distribution of phytoplankton at the ocean-surface. Further, information about fluctuating tidal currents, which distribute food and influence habitat substrate at the seafloor, is only available for some well-studied regions, and has so far not been used for analysing distributional patterns of Antarctic benthic biodiversity. Addressing these issues is important for improving the ability to predict distributional patterns and to increase certainty and robustness of the predictions.

The overall aim of this thesis is to quantify and predict spatial, temporal and structural patterns in the distribution of benthic macro-invertebrate and demersal fish biodiversity on the Antarctic continental shelf, and to improve understanding of the Antarctic benthic ecosystem. In this introduction, I provide an overview of the Antarctic environment, review current knowledge on how environmental conditions influence benthic marine fauna and their distribution, and highlight issues previous studies have encountered when trying to predict the distribution of Antarctic seafloor biodiversity. I focus in part on the role that surface primary production and ocean currents play in determining the availability of food near the seafloor. Further, I review new statistical methods that can be used to map distributional patterns of biodiversity at unprecedented quality and present an outline and aims of the thesis.

The Antarctic environment and its influence on seafloor communities

The Antarctic marine environment is unique in many aspects (Post et al. 2014). Since the disintegration of the former Gondwana continent about 41-28 Ma and the subsequent opening of the Drake Passage, the strong Antarctic Circumpolar Current has isolated the Antarctic continent from the rest of the world (Lawver and Gahagan 2003, Lagabrielle et al. 2009). The continental shelf is relatively deep (~500 m) due to Antarctica's glacial history (Post et al. 2014), and seasonal ice cover means that light-availability, water column stratification and primary-productivity are highly variable (Convey et al. 2014, Post et al. 2014). While melting and freezing processes of sea-ice and ice-shelves influence salinity and current regimes of Antarctic waters, water temperatures are relatively stable year-around (Post et al. 2014). The periodic calving of massive icebergs not only influences ocean currents and the activity of polynyas, but icebergs can scour the seafloor at depth up to 500 m, disturbing the benthic habitat in their path (Gutt 2001). All these environmental parameters can influence species distributions and thus community composition and functioning.

Common factors that influence seafloor fauna include depth (e.g. Gutt and Starmans 1998, Barry et al. 2003, Koubbi et al. 2010, Post et al. 2010), proximity to major bathymetric features such as canyons that provide habitat structure and influence ocean currents (Post et al. 2010), water current speed (e.g. Gambi and Bussotti 1999, Cummings et al. 2010), sediment composition (e.g. Rehm et al. 2006, Choudhury and Brandt 2007, Kröger and Rowden 2008), the frequency of iceberg scour (Gutt 2001) and temperature (e.g. Peck et al. 2004, Griffiths et al. 2017). Depth is regularly found to strongly influence seafloor fauna, such as in the Ross Sea where the density of benthic megafauna (invertebrates and fish larger than 2-3 cm) declines and the abundance of deposit feeders increases with depth (Barry et al. 2003). Depth is linked to a range of environmental parameters, such as long-term sedimentation patterns that are influenced by past patterns of icesheet movement during glacial periods (Post et al. 2011). Depth also influences the quality of food arriving from the ocean surface, because the deeper a site is, the longer biochemical processes can decompose food-particles during their sinking (Suess 1980). However, a comprehensive review of the distribution of benthic assemblages in the Ross Sea showed benthic assemblages cannot be generally related to environmental variables such as depth (Cummings et al. 2010). For example, while depth generally influences water temperatures, spatial patterns in water temperatures in the Antarctic seem more strongly related to seasonal patterns of sea-ice formation that influence the production of cold Antarctic Bottom Water (Clarke et al. 2009). Further, different species within single benthic communities can be affected by environmental variables in different ways and the reliability of a prediction can vary depending on the subset of organisms, the spatial scales and the region considered, and can vary even within regions (Cummings et al. 2010). Part of the reason we do not find consistent relationships between environmental conditions and the distribution of species assemblages might be because many of the environmental variables used in analyses are not directly relevant for the species, but only approximate actually important variables. The availability of food at the seafloor is one important environmental variable that has been missing in analyses to date and has only been approximated using other environmental variables (mainly surface primary production).

The importance of surface-derived food

Most life on the seafloor below the photic zone in which photosynthetic production is possible depends on food derived from the ocean surface (Grebmeier and Barry 1991). Surface productivity in the Southern Ocean can vary greatly as iron, the key limiting nutrient for phytoplankton in the Southern Ocean, and sea-ice cover are patchily distributed in space and time (e.g. Arrigo and van Dijken 2003). In addition, large parts of the ocean surface are ice-covered throughout winter and communities are thought to rely largely on summer influxes (Smith et al. 2006). Among other variables, Thrush et al. (2010) identified sea surface productivity as an important factor influencing beta-biodiversity of coastal benthic assemblages. Similarly, surveys at McMurdo Sound in the Ross Sea indicate strong differences in composition and abundance of benthic assemblages related to differences in advective food supply (Dayton and Oliver 1977, Barry and Dayton 1988). The McMurdo Sound studies found patterns in different benthic communities at two sites correlated with different origins of water currents. Current from under the ice-shelf with low food supply was associated with overall low faunal abundances and a 'worm dominated system' while current from the open ocean with higher food supply was associated with higher faunal abundances and dominated by arthropods. The existence of a link between surface-derived food and the composition of seafloor communities is clear (Dayton and Oliver 1977, Duineveld et al. 2004, Wei et al. 2010, Ruhl et al. 2014), but to date has not been well quantified at regional spatial scales and at fine resolution relevant to management and ecology respectively. Current global models (Laws et al. 2000, Lutz et al. 2007, Siegel et al. 2014) that simulate the export of surface-derived food to the seafloor are developed at a coarse resolution and do not incorporate physical oceanographic processes such as vertical and horizontal currents that may be important in determining the distribution of suspended particles at regional scales (Lampitt 1985, Jahnke et al. 1990). Modelling the transport of primary production to the seafloor may prove to be a key factor in enabling more robust spatial predictions of the distribution of Antarctic seafloor biodiversity and might enable predicting future changes at the seafloor caused by a changing Antarctic icescape.

Statistical tools for predicting spatial and temporal patterns in the distribution of Antarctic seafloor biodiversity

There is a wide range of different statistical tools that can be applied to ecoregionalisations and biodiversity modelling, depending on the aspect of biodiversity being modelled and the datasets available (e.g. Ferrier and Guisan 2006, D'Amen et al. 2017). Choosing suitable statistical tools for analysis is crucial to maximise the use of the often sparse biological data and importantly for making correct inferences about biodiversity patterns (e.g. Warton et al. 2012, Warton et al. 2015a).

Most commonly, modelling the distribution of biodiversity is approached using species distribution models (SDMs) (e.g. Guisan et al. 2002, Lehmann et al. 2002, Guisan et al. 2006, Beger and Possingham 2008, Elith and Leathwick 2009). SDMs allow to map spatial patterns in the distribution of the modelled biological unit based on its response to a suite of environmental factors. There are three main modelling algorithms commonly used in SDMs, namely distance-based techniques, machine learning techniques, and regression-based techniques. While distance-based techniques have stronger limitations for

biodiversity modelling because they reduce multidimensional biological data to single measures of dissimilarity, both distance-based techniques and machine learning techniques can be challenging to interpret because response variables are transformed and/or because an ensemble of trees or hidden layers in neural networks are used to model the data. In contrast, regression-based techniques such as generalised linear models (GLMs) directly relate observations of the abundance or the presence/absence of a single species or a functional or taxonomic unit to a suite of environmental variables (Ferrier and Guisan 2006, Elith and Leathwick 2009). A further advantage is that the mean-variance relationship of the biological data can be specified in a GLM, and a measure of uncertainty can be calculated for the predictive maps (e.g. Hill et al. 2017, Jansen et al. 2018b).

To date, most studies in the Antarctic have focussed on single species distributions of commonly found taxa based on presence-only data (e.g. Gutt et al. 2012, Pierrat et al. 2012, De Broyer et al. 2014). While these studies provide important insight into habitat preferences for the individual species, they do not allow inferences into where and how biodiversity is distributed. Modelling the distribution of many species individually usually is not an option because the majority of marine species are rare, and thus most species cannot be modelled. Community-based analyses can provide insight into the distribution of biodiversity by analysing the dissimilarity between sites, which has been shown at different spatial scales in East Antarctica (Koubbi et al. 2010, Koubbi et al. 2011b). However, with most techniques used to date the species composition of assemblages in identified ecoregions is difficult to dissect because derived values representing the community structure are modelled rather than responses of individual species, and there is no measure of uncertainty associated with the predictions, meaning the confidence in the predicted values is unknown.

More recently, new statistical tools have been developed which allow modelling multiple species simultaneously in a multivariate GLM framework. One particular approach, called Species Archetype Models (SAMs) (Dunstan et al. 2011) group species with similar responses to environmental gradients into ‘species archetypes’ for modelling. SAMs are based on a finite mixture model, where mixing is performed over the individual species’ responses to environmental gradients and each species archetype has an associated GLM that can be used to predict distributions with appropriate measures of uncertainty. The distinct advantage of SAMs is that many rare species, which are usually disregarded in other analyses, are modelled together with more abundant species, allowing a more complete analysis of the species community. Further, SAMs also allow direct interpretation of how individual species respond to different environmental factors and allow quantifying the uncertainty of the predictions.

Aims and overview of chapters

In this thesis, a particle-tracking model is developed to predict the availability of ocean surface-derived food for seafloor communities, and the estimates of food-availability are used in combination with other environmental factors, observations from the seafloor, and quantitative and qualitative models to predict spatial, temporal and structural patterns in the distribution of Antarctic seafloor biodiversity. The study area is the George V shelf in East Antarctica, a region that lies within a recently proposed marine protected area. Despite the focus on this single region, the processes uncovered, and the tools

developed are intended to increase understanding of the functioning of the entire Antarctic benthic ecosystem, and of benthic systems elsewhere.

In **Chapter 2**, an interdisciplinary approach for modelling the redistribution of food-particles from the ocean-surface to the seafloor is developed. The model works by combining satellite estimates of surface-chlorophyll-a with a regional ocean model and particle tracking, validated using diatom abundances from sediment grabs. The work shows how different aspects of food availability at the seafloor directly relate to the abundance and richness of key Antarctic seafloor fauna, namely suspension feeding, deposit feeding, and predatory invertebrates observed from camera images at the seafloor.

In **Chapter 3**, food-availability models are combined with a purpose-built ocean model to map the distribution of important habitat-forming suspension feeders on the George V shelf and used to predict changes in their abundance after a major glacier calving event in 2010. This work provides insight into how changes at the ocean surface influence species communities on the deep seafloor.

Chapter 4 focusses on a more detailed analysis of the distribution of benthic invertebrate diversity on the George V shelf, and on the role that the quality of biological data plays in detecting spatial patterns of biodiversity from environmental data. Combining presence-absence data of invertebrate species and biologically relevant environmental factors, with species archetype models, enables identifying and mapping the distribution of six distinct assemblages of benthic invertebrates in the region. Further, this chapter shows that grouping species by either taxonomic or functional similarity prior to analysis distorts patterns in species distributions and introduces uncertainty into predictions. These uncertainties may have consequences for management and conservation of marine ecosystems, and it is therefore recommended that functional or taxonomic groups are not used on presence-absence data for this kind of analysis.

In **Chapter 5**, the functioning of the Antarctic benthic ecosystem as a whole is investigated. First, a similar approach as in *Chapter 4* is used to identify and map the distribution of five distinct assemblages of demersal fish from benthic trawls. Comparing patterns in the spatial distribution of demersal fish and benthic invertebrates, the distribution of benthic species is then described along four broad habitats characterised mainly by depth and slope of the seafloor. I conceptualise knowledge about the structure and interactions in the Antarctic benthic ecosystem in a qualitative network topology and test a dynamic network model against data about community structure from the species distribution models. This shows how changes in environmental conditions affect the ecosystem, revealing insight into ecosystem functioning.

In the last chapter (**Chapter 6**), the recent advances laid out in this thesis are discussed in the context of biodiversity predictions. In particular, this chapter highlights why biodiversity predictions are important, what commonly limits our ability to predict biodiversity, what recent tools increase our ability to predict biodiversity, and how we might predict biodiversity in the future.

Chapter 2

Abundance and richness of key Antarctic seafloor fauna correlates with modelled food-availability

This chapter has been published as an article under the same title in
Nature Ecology & Evolution **2**, 71-80 (2018)
doi: 10.1038/s41559-017-0392-3

Jan Jansen[1,2], Nicole A. Hill[1], Piers K. Dunstan[3], John McKinlay[2], Michael D. Sumner[2,4], Alexandra L. Post[5], Marc P. Eléaume[6], Leanne K. Armand[7], Jonathan P. Warnock[7+], Benjamin K. Galton-Fenzi[2,4] & Craig R. Johnson[1]

[1] Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia
[2] Australian Antarctic Division, 203 Channel Highway, Kingston TAS 7050, Australia
[3] CSIRO Oceans and Atmosphere, 3-4 Castray Esplanade, Battery Point TAS 7004, Australia
[4] Antarctic Climate & Ecosystem Cooperative Research Centre (ACE CRC), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia
[5] Geoscience Australia, Jerrabomberra Ave & Hindmarsh Drive, Symonston ACT 2609, Australia
[6] Muséum National d'Histoire Naturelle, UMR 7205-ISYEB, MNHN-CNRS-UPMC-EPHE, 57 Rue Cuvier, CP51, 75231, Paris Cedex 05, France
[7] Department of Biological Sciences, MQ Marine Research Centre, Macquarie University, Balaclava Road, North Ryde NSW, 2109, Australia
[8] Department of Geoscience, Indiana University of Pennsylvania, 302 East Walk. 111 Walsh Hall. Indiana, PA 15701 USA

Abstract

Most seafloor communities at depths below the photosynthesis zone rely on food that sinks through the water-column. However, the nature and strength of this pelagic-benthic-coupling and its influence on the structure and diversity of seafloor communities is unclear, especially around Antarctica where ecological data are sparse. Here we show that the strength of pelagic-benthic coupling along the East Antarctic shelf depends on both physical processes and the types of benthic organisms considered. In an approach based on modelling food availability, we combine remotely-sensed sea surface chlorophyll-*a*, a regional ocean model, and diatom abundances from sediment grabs with particle tracking and show that fluctuating seabed currents are crucial in the redistribution of surface productivity at the seafloor. The estimated availability of suspended food near the seafloor correlates strongly with the abundance of benthic suspension feeders, while the deposition of food-particles correlates with decreasing suspension feeder richness and more abundant deposit feeders. The modelling framework, which can be modified for other regions, has broad applications in conservation and management, as it enables spatial predictions of key components of seafloor biodiversity over vast regions around Antarctica.

2.1 Introduction

More than 90 % of the world's ocean floor is found below 200 m depth (Watling et al. 2013). Here, little to no photosynthesis is possible and the diversity of life must ultimately derive energy from imported sources. One major pathway is food raining from the sea surface in the form of particulate organic carbon (POC) (Suess 1980). The existence of a link between export of POC and the composition of seafloor communities, which we refer to as pelagic-benthic coupling (Graf 1989), is clear (Dayton and Oliver 1977, Duineveld et al. 2004, Wei et al. 2010, Ruhl et al. 2014). Surprisingly, however, the strength and nature of the mechanisms determining the availability of surface-derived food at the seafloor has remained largely elusive, inhibiting our understanding of the functioning of the largest ecosystem on Earth. This lack of knowledge is particularly an issue in regions that are difficult to access but support high levels of seafloor biodiversity, such as around Antarctica where 42-56 % of all species (Griffiths et al. 2009), and up to 97 % of species within certain groups (De Broyer et al. 2014, Chown et al. 2015), are estimated to be endemic. In these areas, understanding the spatial distribution of surface-derived food and its relation to seafloor biodiversity is critical for informed conservation and management.

The current evidence describing pelagic-benthic coupling in Antarctic systems is conflicting. On the one hand, highly seasonal light availability, sea-ice cover, and water-column stratification produces distinct phytoplankton blooms with high export ratios to the seafloor which can promote a direct and strong relationship (Smith et al. 2006), as indicated by the abundance of some deposit feeding infauna (Lins et al. 2015, Learman et al. 2016). Conversely, only weak and indirect pelagic-benthic coupling is evident for other benthic fauna such as suspension feeders (e.g. Barry et al. 2003). A further complication is that some benthic species are adapted to seasonal changes in food availability by becoming dormant in winter when food supply is low (Obermüller et al. 2010), or by relying on excess primary productivity stored in 'sediment food banks' that have the potential for resuspension in winter (Smith et al. 2006, 2008).

The ability to model the transport of primary production to the seafloor is key in resolving these complexities.

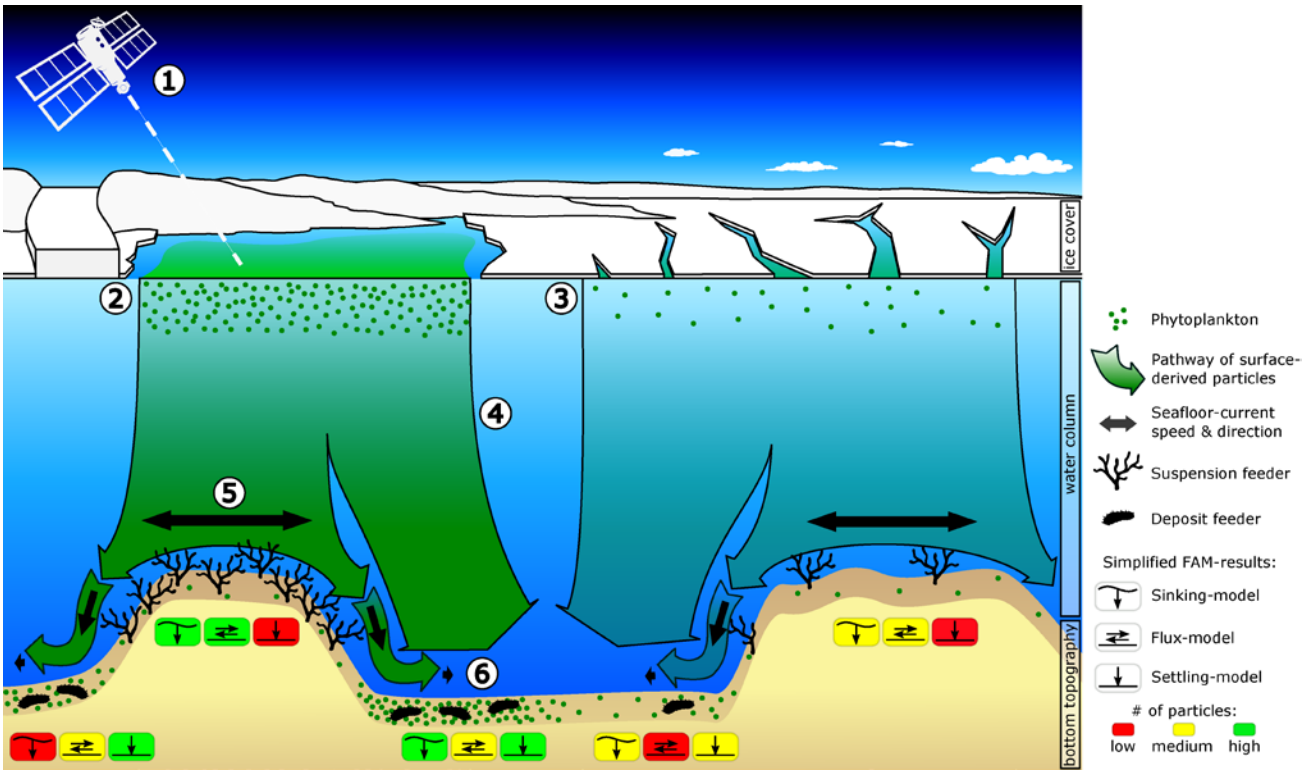


Figure 2.1: Overview graphic summarising general processes involved in the redistribution of surface derived food in Antarctic waters and the link to the seafloor community. In the context of estimating the influence of surface-derived production on seafloor communities, we term our modelling approach a 'Food-Availability-Model' (FAM). Simplified FAM-results are indicated with symbols at the bottom of the graphic. The sinking-model estimates the number of surface-derived particles arriving near the seafloor. The flux-model estimates the number of particles suspended in the fluctuating seafloor-currents. The settling-model estimates the number of particles permanently settling onto the seafloor. **(1)** In highly seasonal regions such as the Southern Ocean, much of the surface production is exported to depth. Here, satellite derived measures of surface chlorophyll-a provide good estimates for spatial patterns of surface production (Huang et al. 2012). **(2)** Coastal Polynyas are areas of ice-free waters with high phytoplankton productivity and high export to the seafloor (Arrigo and van Dijken 2003). They are often found on the leeward side of major glacial features such as the Mertz Glacier Tongue in East Antarctica. **(3)** Other coastal areas are covered by sea-ice for longer periods of the year, and therefore export less surface production to the seafloor. **(4)** During their sinking to the seafloor, surface-derived particles are displaced through ocean currents. In our model, this process is simulated in the sinking-model, while biochemical degradation of particles during sinking is assumed proportional to surface production. **(5)** Seafloor currents, in particular tidal currents, redistribute surface-derived particles along the seafloor, inhibiting permanent deposition on shallower banks. Our research shows areas with more suspended particles harbour higher abundances of suspension feeders. **(6)** In the basins, low current speeds contribute to high sedimentation rates for particles redistributed in seafloor-currents and arriving directly from the surface. In areas of high sedimentation rates, deposit feeders are more abundant and fewer species of suspension feeders can be found.

At a global scale, quantifying POC-export has received much attention in the context of the biological carbon pump. In these approaches the export of POC is modelled as a function of net-primary production (NPP), NPP variability, sea-surface temperature (Laws et al. 2000, Lutz et al. 2007) and, in some cases, trophic interactions (Siegel et al. 2014). These models, however, are usually developed at a coarse

resolution and do not incorporate physical oceanographic processes such as vertical and horizontal currents (Lampitt 1985, Jahnke et al. 1990) that may be important in the distribution of suspended particles at fine and regional scales. Here, we determine the nature and strength of pelagic-benthic coupling across the George V region in East Antarctica (Fig. 2.1 & 2.2) using an approach based on food availability. Our Food-Availability-Model (FAM) aims to estimate the redistribution of surface-derived POC to the seafloor using a combination of remotely sensed estimates of surface chlorophyll-*a* (2002-2007) (NASA Goddard Space Flight Center 2014), particle tracking, and a fine-resolution regional ocean model (Cougnon et al. 2013). We evaluate how well the FAM captures distributional patterns of surface-derived particles using diatom abundances from sediment grabs at the seafloor (details on model components, model-evaluation against observations from sediment grabs, and the assumptions in the modelling are described in sections 2.4.2 and 2.4.4 of the Methods). Our FAM simulates and quantifies the two main physical processes involved in pelagic-benthic coupling, namely sinking of POC from the surface and its sedimentation on the seafloor, and then estimates the horizontal flux of POC along the seafloor as a third process. We then use our models to predict spatial patterns of POC sinking, sedimentation, and horizontal flux across the region. Finally, we quantify the relationship between the three estimates of food-availability (from our spatial models) and the abundance of major groups of seafloor biota derived from underwater camera images, demonstrating the importance of surface-derived POC to the distribution of benthic suspension and deposit feeders on the Antarctic shelf.

2.2 Results

2.2.1 Redistribution of surface productivity to the seafloor

The relationship between multi-year averaged patterns of surface production represented by chlorophyll-*a* (Fig. 2.3a) and the absolute abundance of diatoms at the seafloor interface provided an initial baseline, indicating a weak positive relationship (22 % deviance explained, Fig. 2.3b). Our simplest particle-tracking model, the ‘sinking-model’, represents POC that reaches the seafloor (Fig. 2.3c) by accounting for current-induced horizontal advection during the sinking process across sinking speeds ranging from 100-400 m/day. The best fitting sinking-model had a sinking speed of 300 m/day and marginally improved the statistical fit of the modelled particles to observed diatom abundances, but the relationship is still relatively weak (23.8 % deviance explained, Fig. 2.3d). However, the sinking-model does not account for physical processes at the seafloor, where the speed of seafloor currents can influence the settlement of particles (McCave and Swift 1976) and their resuspension (Lampitt 1985). We incorporated these sedimentation processes in our ‘settling-model’, which determines the number of particles settling onto the seafloor depending on a range of variables including current speed at the seafloor and the number of particles suspended.

The settling-model vastly improved the statistical fit between the predicted relative abundances of particles on the seafloor (Fig. 2.3e) and the observed absolute diatom abundance at the sediment interface, explaining 48.8 % of the total deviance (Fig. 2.3f). Using the output of the 250 and 300 m/day sinking-model resulted in the best fit across the entire spectrum of particle sizes tested

(0.04-0.8 mm; Appendix A Fig. 1), suggesting particles sink quickly from the surface to the seafloor in this region. Our estimated sinking speed is similar to that found for POC in sediment traps from the Antarctic zone (210 m/day) (Rigual-Hernández et al. 2015). We found the best-fitting particle radius for the settling-model to be 0.24 mm, which is larger than that of single cells of *Fragilariopsis spp* (up to 0.1 mm (Beans et al. 2008)), but close to sizes of diatom-aggregates and faecal-pellets that form during the export of phytoplankton blooms (Laurenceau-Cornec et al. 2015).

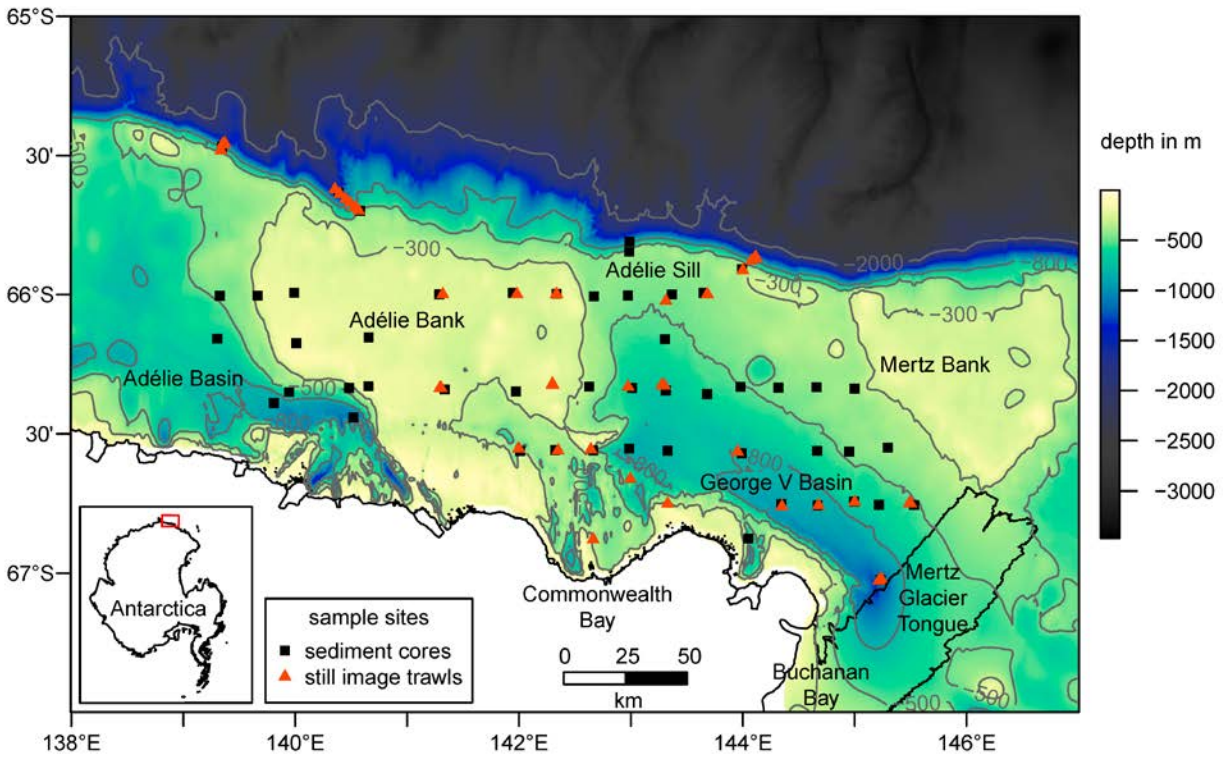


Figure 2.2: Study area showing sample locations, bathymetry (Beaman et al. 2011) with selected contour lines, coastline and major glacial features such as the Mertz Glacier Tongue on the eastern margin of the map. The inset map shows the location of the study area as highlighted by the red box.

2.2.2 Horizontal flux of surface-derived POC along the seafloor

We used the movement of particles from when they arrive on the seafloor (sinking-model) to where they deposit (settling-model) to quantify the horizontal flux of particles in each cell. This third component of the food-availability-model (the 'flux-model') estimates the spatial distribution of horizontal POC-flux (Fig. 2.3g) and represents the amount of suspended food available for suspension feeders such as corals and sponges. While it is not possible to evaluate this model directly because we lack observations of food content in the seafloor currents, we are confident the flux-map well represents suspended food transport along the seafloor given the calibration of the sinking- and settling-models to data from the sediment cores.

It is important to note that the horizontal flux-model represents only the presence of particles moving through environmental grid cells, not how often a single particle has visited a cell through multiple tidal cycles. This approach avoids distortion of the count of particles at cell-boundaries. To approximate the repetitive movement of particles between cells we used the strength of residual

currents from the ocean model. Stronger fluctuations (tides) indicate that particles are likely to remain suspended longer, meaning they are also available as food for suspension feeders for longer.

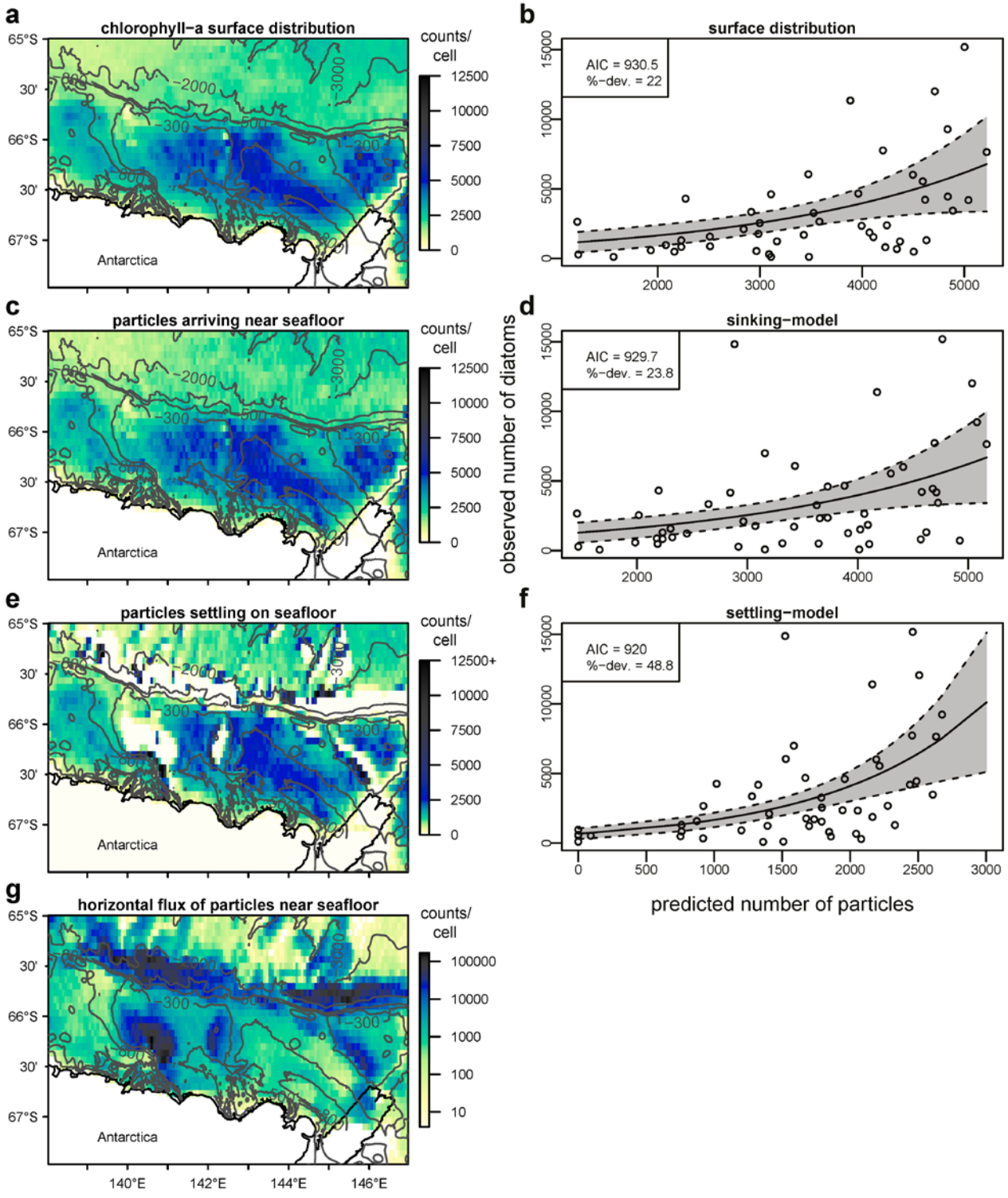


Figure 2.3: Results of the particle tracking models. **a/c/e**) Predicted distribution of surface-derived particles in the study area using simulations with different levels of complexity. Contour lines at 300, 500, 800 and 2000 m depth are given to highlight bathymetric features. **a**): Multi-year averages (2002-2007) of surface chlorophyll-a concentration as observed from satellites, transformed into a representative distribution of particles for particle-tracking. The surface distribution can be used as a first, simple, non-modelled approximation of the distribution of POC on the seafloor **c**): Particle distribution

after accounting only for horizontal advection during the sinking process at a sinking speed of 300 m/day. **e**): Particle distribution map resulting from the settling-model with the best statistical fit to absolute diatom abundances in sediment grabs. The particle distribution is the result of consecutive application of a sinking-model with a 300 m/day sinking speed and, to account for sedimentation processes, a settling-model with particle radius of 0.24 mm. The colour-scale of the settling-map slightly differs to facilitate comparison of spatial patterns between the maps. Further, nine outlier grid-cells that contain values higher than 12500 particles (up to 29372), are coloured as '12500 +'. **b**/**d**/**f**) Statistical fit of a negative binomial generalised linear model for the predicted particle distributions to the observed diatom abundances from 52 sediment grabs. The shaded area marks 95 % confidence interval of the estimated mean. AIC = Akaike Information Criterion, %-dev. = percent-deviance explained by the model. **g**) Map of the estimated horizontal flux of particles along the seafloor. Note how this differs from the distribution of particles at the surface (in **a**) and arriving near the seafloor (in **b**).

2.2.3 Spatial patterns in the distribution of surface-derived POC

The spatial pattern of particles arriving near the seafloor is almost identical to the distribution of time-averaged surface chlorophyll-*a* (*cf.* Fig. 2.3a/c, Pearson's R= 0.967), presumably due to the fast sinking rate of particles in the sinking model and the relatively small average current speeds in the open water column in summer (Appendix A Fig. 2b). On the shallower sections of the shelf, diatom aggregates may reach the seafloor as quickly as two days following a bloom, a timescale similar to previous estimates for the Southern Ocean (Laurenceau-Cornec et al. 2015, Rigual-Hernández et al. 2015). Therefore, in areas with little average current on the shelf, such as the George V shelf (Appendix A Fig. 2), patterns of surface chlorophyll-*a* provide a good approximation of the pattern of particles arriving and temporarily depositing on the seafloor.

The estimated spatial distribution of particles from the settling-model is reasonably similar to the distribution of particles arriving near the seafloor (*cf.* Fig. 2.3c/e, Pearson's R= 0.564) despite the strong influence of seafloor-currents. This similarity is partly attributable to the location of the Mertz Polynya, a hotspot of surface phytoplankton productivity (Arrigo and van Dijken 2003, Beans et al. 2008, Arrigo et al. 2015), which is largely situated above the deep George V Basin (Fig. 2.2) where currents are relatively slow and deposition is high (Beaman and Harris 2003). In contrast, the spatial distribution of horizontal POC flux differs substantially to both the distribution of particles reaching the seafloor and the particles settling. Horizontal POC flux along the seafloor is linked to seafloor morphology, presumably due to the influence that seafloor bathymetry has on seafloor currents (Canals et al. 2006). A particularly strong horizontal flux is predicted on shallow banks (200-300 m depth) and through slope canyons, whereas in the deep George V Trough horizontal flux is predicted to be three to five orders of magnitude lower with concomitant higher deposition. Acoustic data from the region support these results; thick sediments (up to 35 m (Beaman and Harris 2003)) comprised of siliceous mud and diatom ooze (Harris et al. 2001) characterise the Mertz Drift in the western part of the George V Basin, while the Mertz and Adelie Banks (Fig. 2.2) show little evidence of sediment deposition (Beaman and Harris 2003). Further, the channel network along the slope is subjected to strong down-slope currents resulting in widespread evidence of erosion (Caburlotto et al. 2006).

Unsurprisingly, the horizontal flux-map shows similarities to a map of averaged absolute seafloor current speeds (Appendix A Fig. 2a, Pearson's R= 0.481), reflecting that seafloor-currents are the main process redistributing surface-derived POC. However, while seafloor current speed is substantially

higher along the shelf break, this does not result in a higher flux of particles because of relatively low delivery rates of particles to this region (Fig. 2.3c). In contrast, very high particle flux is indicated on the shallow banks on the shelf. This finding emphasises that both information on patterns of surface productivity and seafloor currents is required to estimate the availability of suspended food above the seafloor, as neither on their own is sufficient.

2.2.4 Influence of redistributed surface production on seafloor biodiversity

The strength and nature of pelagic-benthic coupling is dependent on the type of benthic organisms considered, meaning processes involved in the redistribution of surface-derived food can have varying importance for different types of benthic organisms. Several studies (Dayton and Oliver 1977, Barry and Dayton 1988, Gutt et al. 2013c) indicate that areas with slow currents and higher deposition are associated with impoverished epibenthic communities dominated by mobile deposit feeders (DF) such as holothurians, while in areas of stronger currents and food enrichment, benthic suspension feeders (SF) such corals, sponges, and crinoids dominate. We analysed the relationship between our estimates of food availability at the seafloor and the abundance and species richness of epibenthic SF, DF, and predators determined from still images taken from cameras attached to benthic trawls in 2007-2008 (Hosie et al. 2011). Since biota abundances and richness might be influenced by several co-variables simultaneously, in addition to food availability, we also considered ocean current speed, depth, surface productivity, and slope of the seafloor via multiple linear regressions weighted by the number of images for each site.

As indicated by previous studies (Dayton and Oliver 1977, Barry and Dayton 1988, Gutt et al. 2013c), we found that different functional groups respond differentially to the estimates of food availability. Most notably, horizontal flux of food along the seafloor is an important variable explaining the cover of SFs (Fig. 2.4b: $t_{37} = 5.74$, $p < 0.001$), but not DFs (Fig. 2.4g/h/i), which appear unable to profit from abundant but inaccessible suspended food. In addition to horizontal flux, tidal current speeds are also an important variable for SF (Fig. 2.4c: $t_{37} = 4.58$, $p < 0.001$). These two variables (horizontal flux and tidal current speed) in combination explain where the food is moving and its residence time across the study zone. Horizontal flux and tidal current speed have previously been identified as playing a major role in influencing the abundance and distribution of benthic suspension feeder communities (Roberts et al. 2006, Post et al. 2010), but until now have not been quantified at scales relevant for conservation. We also found a strong effect of depth on the abundance of SFs. This relationship is thought to be of variably strong importance in Antarctica (Cummings et al. 2010, Gutt et al. 2013c) and in other parts of the world (e.g. Beazley et al. 2015) implying that seafloor depth can act as a proxy for several important environmental variables such as biochemical degradation of surface derived food (e.g. Goutx et al. 2007).These three variables (horizontal flux, tidal current speed, depth) combined explain 68 % of SF-abundance (adjusted-R^2= 0.677), 8 % more than a regression model that does not consider food availability (adjusted-R^2= 0.593). Assessing variable importance by bootstrap resampling confirms the high importance of the three selected terms relative to all other covariates (Appendix A Fig. 3a), and highlights the stability with which these three variables can be used for spatial predictions of SF across the study area.

Habitat forming SF provide spatial structure and microhabitat for other species, and are therefore a critical component of epifaunal seafloor biodiversity. They are also the most abundant and species rich functional group in our dataset, and show a strong positive relationship between abundance and species richness (Fig. 2.5). Interestingly however, species richness does not directly relate to the horizontal flux of food (Fig. 2.4d/e/f). Instead, the presence and absence of suspension feeding species is positively related to the vertical flux of particles from the sinking-model (Fig. 2.4e), and negatively related to the long-term sedimentation of those particles (Fig. 2.4f), indicating possible smothering effects and/or a lack of suitable substratum in high sedimentation environments. Therefore, while the horizontal flux of food influences the abundance of the habitat forming seafloor fauna, the species richness of this community seems to be more related to variables impacting on the seafloor, similar to recently suggested relationships in the northwest Atlantic (Lacharité and Metaxas 2017).

In contrast to the SFs, we find no positive response in the abundance of DFs to the flux of suspended food (Fig. 2.4g/h/i), but a positive response to the number of particles settling on the seafloor, in line with expectations as this functional group feeds on material deposited on the seafloor and cannot access suspended particles. Additionally, both abundance and richness of DFs decrease with depth, presumably due to the same mechanisms as described earlier. Surprisingly, we find a negative relationship between DF abundance and surface production (Fig. 2.4i) and a decrease in richness with the amount of suspended food (Fig. 2.4k). However, interpreting this result is not straightforward for several reasons. In this study we lack data on infauna, which can also demonstrate strong pelagic-benthic coupling (Lins et al. 2015). Further, in the present study there were few macrobenthic species with relatively low abundances classified as ‘pure’ DFs. Some deposit feeders manifest other feeding modes such as being opportunistic scavengers, and were excluded from the DF category. There was only a weak relationship between physical environmental variables and the abundance of predators (Appendix A Fig. 6).

2.3 Discussion

Our models and ecological data show that pelagic-benthic coupling in Antarctica is primarily driven by depth, surface productivity and the redistribution of that production through seafloor currents, but that it varies depending on the types of benthic organisms considered. Our work supports previous suggestions of the importance of horizontal food-transport along the seafloor (Lampitt 1985, Jahnke et al. 1990).Patterns of surface productivity alone and currently available POC-models (Lutz et al. 2007, Siegel et al. 2014) , neither of which capture particle movements through currents, are unlikely to reasonably estimate depositional patterns of POC on the seafloor at regional scales making it necessary to include tide-resolving fine resolution ocean models. The ability to incorporate these physical processes and quantify their importance in estimating the redistribution of surface productivity highlights the significant step forward of our fine-scale modelling approach.

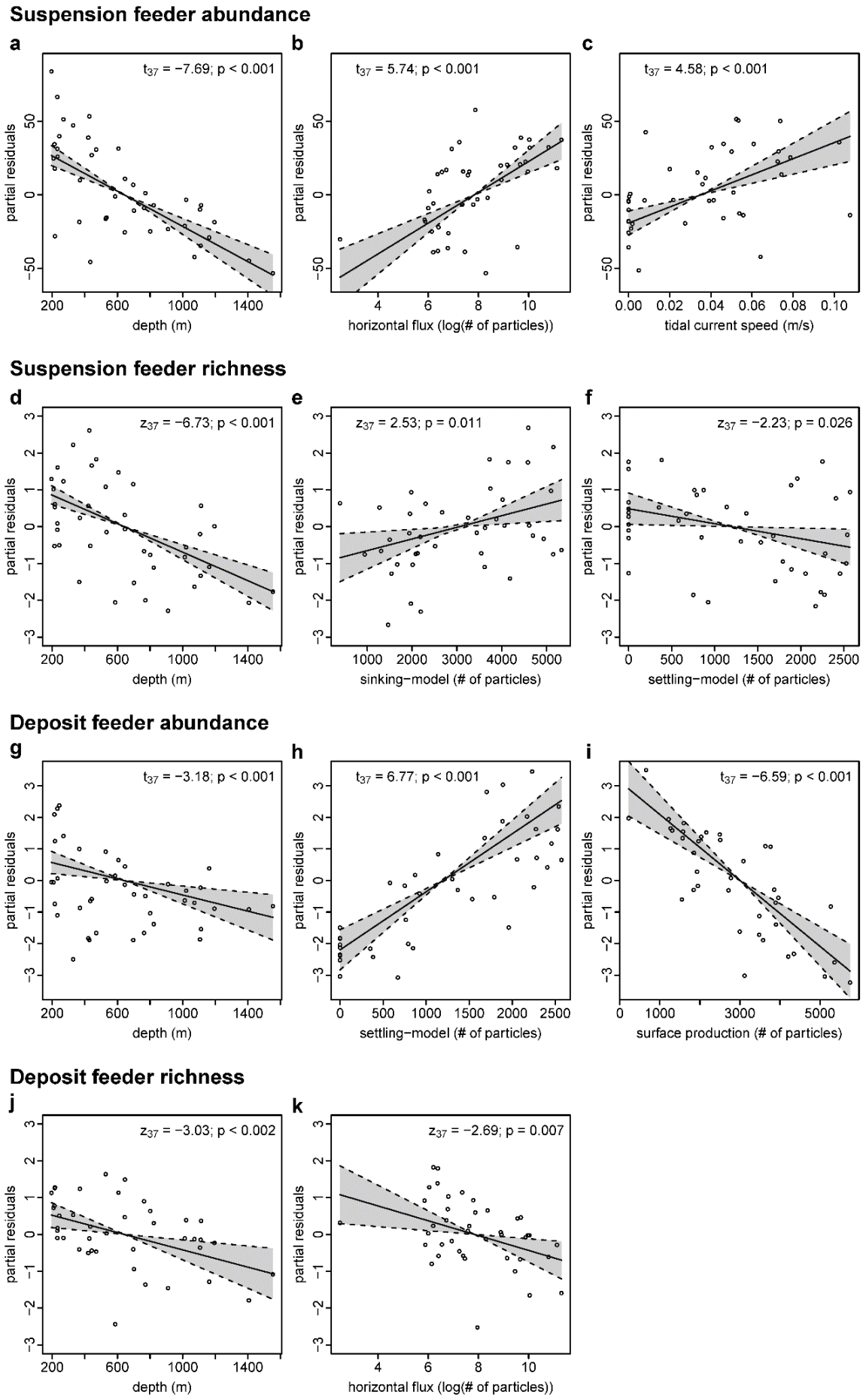

Suspension feeder abundance
a
t_{37} = −7.69; p < 0.001
partial residuals
depth (m)
b
t_{37} = 5.74; p < 0.001
horizontal flux (log(# of particles))
c
t_{37} = 4.58; p < 0.001
tidal current speed (m/s)
Suspension feeder richness
d
z_{37} = −6.73; p < 0.001
e
z_{37} = 2.53; p = 0.011
sinking−model (# of particles)
f
z_{37} = −2.23; p = 0.026
settling−model (# of particles)
Deposit feeder abundance
g
t_{37} = −3.18; p < 0.001
h
t_{37} = 6.77; p < 0.001
i
t_{37} = −6.59; p < 0.001
surface production (# of particles)
Deposit feeder richness
j
z_{37} = −3.03; p < 0.002
k
z_{37} = −2.69; p = 0.007

Figure 2.4: Relation between faunal abundances and richness from benthic images and environmental variables. **a**-**c**) Suspension feeder abundance (adjusted-R^2= 0.677); **d**-**f**) suspension feeder richness (%-deviance explained = 58.9); **g**-**i**) deposit feeder abundance (adjusted-R^2= 0.718) and **j**/**k**) deposit feeder richness (%-deviance explained = 46.9). The graphs show partial residuals and fitted regression lines with 95 % confidence intervals (shaded area) for weighted multiple linear regressions on selected environmental variables (n = 41). A linear model with data points weighted by the number of images taken per site is used for the percent-cover relationship, and a negative binomial generalised linear model is used for the species richness relationships with an offset-term to correct for the number of images. z = ratio of the coefficient to the standard error of the predictor variable

Variation in absolute diatom abundances on the seafloor that remain unexplained by our models likely stem from the space-time complexity of sinking and sedimentation processes not captured by our models, such as small scale variability in current speeds or the variable composition of species in the sinking diatom aggregates. Our models are technically capable of incorporating other potentially important terms for POC-export, such as the attenuation of POC with depth, primary production from sea-ice algae and spatial differences in zooplankton grazing pressure. We chose not to include these terms to keep the model as simple as possible and to avoid including large numbers of parameters that are difficult to validate. Currently, reliable spatial estimates do not exist for either sea-ice algae export or zooplankton grazing. Although Antarctic sea ice algae production is conservatively estimated to be only around 12 % of total primary production in the sea-ice zone (Saenz and Arrigo 2014), this additional export means our models are likely to underestimate particle numbers in areas that are covered by sea-ice for longer periods of the year. The high sinking rates for particles suggests zooplankton grazing has a smaller influence on POC-export in this region than elsewhere. In the future, we may be able to better validate some of these parameters, and some will certainly become available at a higher resolution, meaning their information can then be included in our approach. The fact that our models perform so well even though they do not include these terms, suggests that the most important physical processes in pelagic-benthic-coupling are captured in the model.

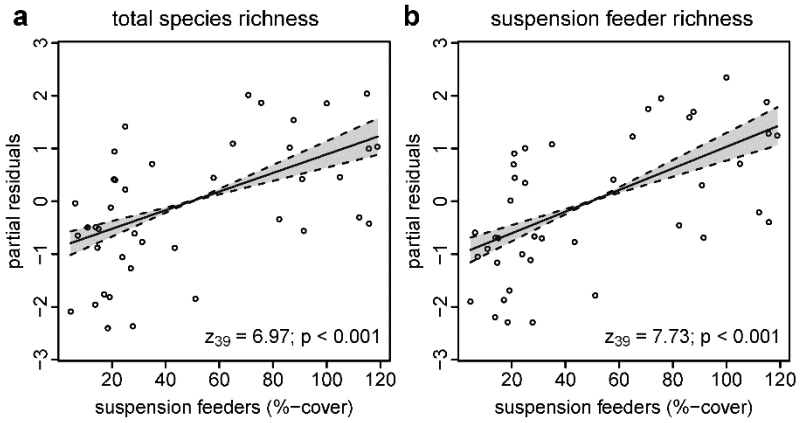


Figure 2.5: Relationship between suspension feeder cover and number of species observed. **a**) Number of all benthic species observed (%-deviance explained by model = 49.9); **b**) number of suspension feeding species observed (%-deviance explained by model = 54.2). Most of the macroinvertebrate species observed are suspension feeders, therefore the relationships look very similar. Shown are the partial residuals and fitted regression lines with 95 % confidence intervals (shaded area) from an analysis using negative binomial generalised linear models (n = 41). An offset-term is included in the analysis to correct for the number of images taken at each site. z = ratio of the coefficient to the standard error of the predictor variable.

Previous studies of Antarctic pelagic-benthic coupling are missing quantitative estimates of horizontal food-transport, and therefore they largely misrepresent the importance of surface productivity for seafloor communities. Further, the time scales at which sessile benthic communities respond to food availability differ to the time scales for which in-situ measurements of coupling, such as sediment oxygen demand are usually obtained (Renaud et al. 2008). This mismatch may distort both estimates and interpretation of the nature and strength of pelagic-benthic coupling. Our results indicate that coupling of pelagic productivity to benthic suspension feeders in Antarctica is strong and direct, but that this will likely only be detected when accounting for the redistribution of surface-derived particles by seabed currents, as we have done here.

We suggest that our modelling approach should be widely applicable around the Antarctic margin because of similarities in the environmental setting (Fig. 2.1). Coastal polynyas provide longer than average ice-free waters, marking hotspots in primary productivity (Arrigo and van Dijken 2003). Shelf troughs are areas of high sediment deposition and accumulations of biosiliceous components, while the influence of strong bottom currents on shelf banks and within slope canyons is evidenced by coarser grain sizes with lower biogenic content (Mccoy 1991, Post et al. 2014). However, application of our approach in a non-Antarctic context would need to be considered carefully because global assessments of seafloor sediments show a large contribution of other biogenic components (primarily carbonates) and terrigenous material in many areas (Dutkiewicz et al. 2015). In these areas, diatom concentrations in surface sediment would not be as useful to calibrate models as we have done for the Antarctic shelf.

Food is a fundamental requirement of life, and its availability determines the distribution of all species. Here we have successfully quantified and mapped relevant metrics of food availability at the seafloor and verified their importance in explaining patterns in the abundance and species richness of suspension and deposit feeders that comprise a large component of seafloor biodiversity in Antarctica. Our work enhances understanding of the mechanisms underpinning pelagic-benthic coupling below the photosynthesis zone, highlighting the important role of seafloor currents, and provides a modelling approach that can be modified for other regions. The relationships that we have identified, in combination with our maps of food availability, have broad application in the conservation and management of Antarctic seafloor biodiversity as they enable (1) the ability to more confidently map seafloor communities across regions where empirical sampling is difficult and costly; (2) more accurate assessment of the representativeness of current and planned marine protected areas (MPAs) in Antarctica; and (3) evaluation of the robustness of MPAs against predicted future changes in ocean current patterns and surface productivity as a result of warming oceans and changes in the polar cryosphere (Peck et al. 2010).

2.4 Methods

2.4.1 Study area

Our study area is the George V continental shelf and slope in East Antarctica, spanning latitudes 139°E to 147°E from the Antarctic coastline to the shelf break at around 65.5°S. Water depth on the shelf is typically 500-700 m, punctuated by bathymetric features including the Mertz and Adélie Banks (200-

250 m depth) and the George V and Adélie Basins (depths up to 1300 m) (Fig. 2.2). The inner shelf and the shelf break are incised by a number of depressions and canyons. At the time of data collection, the oceanography in this area was mainly influenced by the Mertz Glacier Tongue and the adjacent Mertz Polynya (Cougnon et al. 2013), an area of ice free water of around 23,300 km^2 centred at about 67°S and 145°E (Massom et al. 2001). The polynya was sustained by strong and persistent katabatic winds draining into Buchanan Bay that rapidly form sea-ice and remove it from the near shore, thereby influencing the water properties and driving water circulation (Massom et al. 2001). The ice-free waters in polynyas are common around the Antarctic shelf and, compared with adjacent shelf areas, support a relatively long growing season of phytoplankton (Sambrotto et al. 2003, Beans et al. 2008) resulting in higher average productivity near polynyas (Arrigo and van Dijken 2003)(Appendix A Fig. 7, Appendix A Fig. 8). On the George V shelf, the phytoplankton community varies spatially and temporally in abundance and composition, notably with higher abundances near the Mertz polynya (Beans et al. 2008). Overall, as occurs in other regions around Antarctica, phytoplankton composition of blooms is generally dominated by diatoms of the genus *Fragilariopsis* (Armand et al. 2005, Beans et al. 2008).

2.4.2 Particle-flux model and environmental forcing

We apply a particle tracking approach combined with a statistical model to estimate spatial patterns in the flux of particulate organic carbon (POC) to the seafloor. From a seeded distribution of particles at the surface, each particle is tracked individually from its original position to its final destination on the seafloor given a range of sinking speeds of particles (described in section 2.4.2-c) and the speed and direction of currents (described in section 2.4.2-b). We developed two separate models to describe the physical processes involved in the horizontal and vertical advection of surface-derived particles namely a *sinking-model* that describes the sinking of particles from the surface waters to the seafloor; and a *settling-model* that builds upon the output from the sinking-model and describes the sedimentation processes that are involved when particles deposit from the near-seafloor layer to the seafloor. The inputs and specifics for each model are described in section 2.4.2-c and the statistical evaluation against seafloor surface sediment samples in section 2.4.4-a.

2.4.2-a Surface-chlorophyll-a, net-primary-production and export

The seeded particle distribution for the tracking in the models is based on measures of ocean colour derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua) (NASA Goddard Space Flight Center 2014). We used Level-3 binned daily remote sensing reflectance, provided at a resolution of 4 km equal-area bins. To avoid significant underestimation of chlorophyll–*a* concentrations at high latitudes, we corrected the values for Southern Ocean application using the algorithm in Johnson et al. (Johnson et al. 2013). Daily measures of surface chlorophyll-*a* were averaged for southern hemisphere spring, summer and autumn in each year for the period between September 2002, when the first satellite data is available, and December 2007, just before sediment core data for model evaluation were collected (see section 2.4.2-c).

We assume the distributional patterns of surface chlorophyll-*a* represent the patterns of exported production from the surface. We use surface chlorophyll-*a* (chl-*a*) rather than net-primary-production (NPP) or NPP-export, as the starting point for our models for several reasons. Our estimates of chl-*a* use an algorithm whose parameters are tailored and validated for the conditions in the Southern Ocean

(Johnson et al. 2013) while global NPP estimates are not. Other regions of the Antarctic (e.g. West Antarctic Peninsula (Huang et al. 2012)) show a high correlation between satellite estimated chl-*a* and measured NPP indicating it is reasonable to consider chl-*a* as a proxy for NPP. We also refrain from using currently available global algorithms that calculate carbon export, because they are usually based on global estimates of NPP and modified by factors such as seasonal variability index and sea-surface temperature (Lutz et al. 2007). While these models are excellent at discriminating between flux patterns in different regions (i.e. high flux following blooms in polar regions, low flux in temperate regions), seasonal variation is uniformly high within our region due to ice-cover in winter and we therefore expect that a high proportion of the surface production exports to depth.

Because we do not account for a range of processes that can influence the absolute values of exported carbon (e.g. attenuation with depth), we present relative values instead for the estimated flux-patterns.

2.4.2-b Water currents and bathymetry

Current speeds and directions used to calculate vertical and horizontal advection of suspended particles in each year are derived from a tide-resolving oceanographic model for the George V shelf developed by Cougnon et al. (2013) from Galton-Fenzi et al. (2012b) based on the Regional Ocean Modelling System (ROMS) (Shchepetkin and McWilliams 2005). The oceanographic model ran for the years 1992-2007 in time-steps of 6 hours, and encompassed the area from the Antarctic coastline to the deep ocean at 62.72°S, and from 135.77°E (west of the French base, Dumont D'Urville) to 158.08°E (east of George V Land (Cougnon et al. 2013)). The domain has a horizontal resolution of about 2.16 km at the southern boundary and 2.88 km near the northern boundary with 31 layers for the vertical grid, arranged to give higher resolution near the bottom and the top of the water column. Bathymetry in this oceanographic model is based on RTopo-1 (Timmermann et al. 2010) and modified to include 250 m-resolution data from Beaman et al. (2011). As noted in Cougnon et al. (2013), results from a different version of this ocean model were compared to summertime shipboard observations and year-long mooring data in the Adelie sill, and were found to accurately reproduce the seasonality and circulation of dense shelf water within the depression.

For the particle tracking we chose four consecutive time-slices of the ROMS-model for each summer season. We used the four consecutive time slices with the strongest differences in current direction and speed, to ensure that each time slice adequately captures one full tidal movement (a 6h time-slice with 3 hours of incoming tide and 3 hours of outgoing tide would show very little current speed). Current speeds and directions for the four time-slices were consistent across years, apart from 2006, which showed very odd and unexplainable current directions and so was excluded from analysis. We averaged current speeds and directions in the matching time slices between years to allow inclusion of 2006 surface productivity in the analysis. For the biodiversity analysis (Section 2.4.4-b), we calculated temporal averages of current strengths for the southern hemisphere summer (21st December to 21st March) for each cell above the seafloor in the following way:

Temporal mean current speed: $\bar{V} = \sqrt{\bar{u}^2 + \bar{v}^2}$

Absolute current speed: $\overline{|V|} = \sqrt{\overline{|u|}^2 + \overline{|v|}^2}$

Residual current speed: $V` = \overline{|V|} - \bar{V}$

where *u* is the current speed on the north-south axis and *v* is the current speed on the east-west axis. The residual current speed mainly reflects tidal currents, but can also incorporate longer-term fluctuations and eddies.

2.4.2-c Particle-tracking

For seeding the particle-tracking model, we transformed the 4 km-resolution grids of seasonal chlorophyll-*a* averages into a relative number of particles per ROMS cell using a random Poisson-point-process. This process preserves the spatial pattern observed in chlorophyll-*a* concentration across the study area/domain. The maximum number of seed particles was around 3 million for summer averages, but several orders of magnitude lower for spring and autumn averages due to lower chlorophyll-*a* concentrations. Particle tracking was done in 30 min. time-steps, where at each time-step the location of each particle with respect to the ROMS-cells was calculated in order to get updated water current speed and direction for advection of the particles during the following time-step. Particles were stopped when they either moved out of the study area or matched the stopping criteria for the respective model, described in the sections below. The resulting particle distributions from each model-run were back-transformed into a grid with a resolution of 1/15 degrees.

For the particle tracking, software was developed in R Version 3.2.0 (R Core Team 2016) using packages 'raster' (Hijmans and 2015), 'ncdf4' (Pierce and 2014), 'nabor' (Elseberg et al. 2012), 'geostatspat' (Brown 2015) and 'spatstat' (Baddeley and Turner 2005) and is available as the package 'ptrackr' (Jansen and Sumner 2017) at www.github.com/janjansen86/ptrackr.

Sinking-model

In the sinking-model, particles simply sink from the surface to the seafloor while being subject to horizontal and vertical advection. In addition to the advection determined by the ROMS model output, a key parameter determining the trajectory of particles is the sinking speed. We used eight different sinking speeds for the particles: 100, 150, 200, 250, 300, 350 and 400 m/day. These sinking speeds are in the range of sinking speeds likely to occur for POC in the study area, taking in to account the composition of phytoplankton species and size of aggregates at the surface (Beans et al. 2008, Laurenceau-Cornec et al. 2015). Particles were considered precipitated when their depth equalled the depth of the seafloor at the respective ROMS cell.

Settling-model

The settling-model accounts for the fact that once particles reach the seafloor they do not necessarily settle permanently, primarily due to high floor current speeds that can maintain particles in suspension in some areas. The settling-model uses the resulting particle distribution from the sinking-model (all years combined) as its input and applies sedimentation processes (McCave and Swift 1976) to calculate where particles are most likely to settle (similar to previous applications of this process (Warner et al. 2008)).

In order to calculate the precipitation rate p' (the fraction of particles settling from the suspension to the seafloor) we follow the reasoning from McCave and Swift (McCave and Swift 1976) in a simplified manner, as follows:

$$p_0 p` = p_i C W_d \left(1 - \frac{U^2}{U_c^2}\right)^2$$

where p_0 is the density of seawater (1030 kg/m^3) and p_i is the density of the settling particles, held constant at 1100 kg/m^3, an average of the values described for nine different marine diatoms (Van Ierland and Peperzak 1984). We are aware that Antarctic diatoms are likely heavier than other marine diatoms, but have found no other literature where such values are presented (greater values for the density will not affect the spatial patterns of the modelling results, but will decrease the estimated best-fitting size of particles in the model). C is the concentration of particles/ROMS-cell, W_d the velocity at which particles settle onto the seafloor (one of the six sinking velocities used in the sinking-models), U the horizontal velocity given from ROMS for each cell at the layer above seafloor. U_c is the critical velocity, above which no sedimentation occurs, and calculated by the following expression:

$$U_c^2 = \frac{0.05(p_0 - p_i) g 2 r_c}{p_0 C_d}$$

where g =9.81 m/s^2, and the constant drag coefficient C_d =2.5x10^{-3}. The effective radius of settling particles r_c, which is the radius of a sphere having the same volume as the idealised disc shaped diatom is calculated as

$$r_c = \left(\frac{3}{2}\varepsilon\right)^{\frac{1}{3}} r$$

where r is the radius of the particles and the aspect ratio ε=1 for an idealised sphere in our modelling.

The settling-model was run with different particle radii ranging from 0.16 mm to 0.40 mm in 0.04 mm steps. Output from the settling-model was evaluated as described in section 4.1.

Horizontal flux model

The settling-model can also be used to calculate the relative amount of suspended particles passing over an area of seafloor. This is achieved by accumulating the horizontal transgression of particles within grid cells that occurs after particles arrive near the seafloor but before settling permanently. We term this the 'horizontal flux'. Due to computational constraints, to keep assumptions concerning the sedimentation and resuspension during the simulated tidal movements to a minimum, and to avoid artefacts on the count of particles at cell boundaries, particles repeatedly visiting the same cell were only scored as a single visit. Therefore, results from the horizontal flux model cannot be used to estimate how long particles stay/fluctuate in an area, but instead reflect the spatial distribution of particle trajectories. Since the ROMS provides information about the spatial distribution and strength of tidal currents, this can be combined with results from the horizontal flux model to provide ecological insights into food availability as a measure of particle trajectories and retention time in the cells. It would be desirable to obtain empirical measurements of horizontal particle flux on the seafloor for validation of the horizontal flux model, but obtaining these data in such a remote location is difficult. Therefore, we are only able to indirectly validate this model using the settling-model and the diatom abundances.

2.4.3 Biological data collection

Biological data were collected during the Collaborative East Antarctic Marine Census (CEAMARC) for the Census of Antarctic Marine Life in December 2007 to February 2008 (Hosie et al. 2011).

2.4.3-a Sediment grabs and diatom abundances

Seafloor sediment samples were collected from 53 sites between 153 m and 1428 m depth. Sediment grabs were taken using a box core, apart from 4 sites where more gravelly sediments required the use of a Van Veen grab sampler. A top scrape (<2 mm) was subsampled from the sediment core. One sample was excluded from the analysis due to poor recovery of the surface sediments. We are confident the subsample reasonably well represents modern sedimentation rates because sedimentation rates from calypso cores collected along the George V coast yield estimates of 0.35 cm/yr (Crosta et al. 2005), 0.4 cm/yr (Crosta et al. 2007) and 0.52 cm/yr (Denis et al. 2009), suggesting that our diatom counts may be representative of a single to a few years of accumulation in the deep basins.

Photographs were used to visually verify good surface recovery of all samples. Surface sediment scrapes were freeze-dried, and ~0.5 g was subsampled for analysis. From the 0.5 g sample, a known volume of between 125 and 250 µL of diatom suspension was further sub-sampled. Slides were prepared according to Rathburn et al. (1997) and coverslips were affixed to slides using Norland Optical Adhesive (NOA 61). In each sample, 500 valves were identified to species level according to Tomas (1997) and Armand and Zielinski (2001). Only planktonic species were used to calculate the absolute diatom abundance (ADA) as a function of the original dried weight using the following equation:

$$ADA = \frac{n_D * A_{petridish}}{n_F * A_{view} V_{Sub}} * \frac{50ml}{M_{Sed}}$$

where n_D is the number of planktonic diatoms counted, n_F is the number of fields of view counted, $A_{petridish}$ is the petri dish area in mm^2, A_{view} is the field of view area in mm^2, V_{Sub} is the subsample volume in mL and M_{Sed} is the dry sediment mass in g.

2.4.3-b Still Imagery and benthic invertebrates

Detailed underwater still images were obtained from a forward facing 8 megapixel Canon EOS 20D SLR with two speedlight strobes, mounted on a beam trawl. Transects at 32 sites were mostly between 4-6 km long, with some exceptions ranging between 3-16 km. The trawl was controlled using a deck winch. Pictures were taken every 10 seconds. Fauna was identified to the highest taxonomic resolution possible. Where species identification was not possible, specimens with similar overall appearance were grouped into morphotypes (operational taxonomic units). The bottom third of each image was scored. For each image, the abundance of each species/morphotype was estimated within 5 % bins from 0 % to 50 % and 10 % bins from 50 % to 100 %. Using their taxonomy and body-type along with expert knowledge, the fauna was then classified into three broad functional groups; suspension feeders, deposit feeders and predators. We excluded two morphotypes from analysis for which a clear identification of the feeding types was not possible.

2.4.4 Statistical analyses

2.4.4-a Particle-flux model evaluation against diatom data

We used planktonic diatom absolute abundances from surface scrapes of sediment grabs (sediment grab collection, processing and diatom enumeration is described in 2.4.3-a) to evaluate and optimise parameters in the particle tracking models. The strong seasonal phytoplankton blooms in the Southern Ocean result in large seasonal downward fluxes of POC (Smith et al. 2006). Diatoms are a major component of these blooms and as a result, make up the majority of POC in the siliceous mud and ooze dominated surface sediments (Domack and Anderson 1983, Dutkiewicz et al. 2015). Our data shows carbonate abundance in the sediments is very low compared to biogenic silica (Post et al. 2011), and therefore the spatial patterns of diatom abundance are well representative of the overall potential POC flux to the seafloor.

In a combined particle tracking and statistical approach, we fitted generalised linear models with a negative binomial distribution to test the relation between observed diatom abundances and the particle tracking results for each combination of model-parameters. We extracted values for the predicted particle abundances from the environmental grid cells corresponding to the diatom seafloor sample locations in each map/model. We tested the statistical fit for different values in the sinking speed (sinking-model) and in the particle size (settling-model) and used lowest AIC (Akaike Information Criterion) as an indicator of the best model. The parameter values resulting in the best statistical fit of the settling-model were used to generate the maps of POC flux.

2.4.4-b Biodiversity analysis

To test whether there is a link between food availability (as estimated with our particle-tracking models) and epibenthic organisms we related the abundance of each functional group and the total number of benthic invertebrate species (operational taxonomic units, Section 2.4.3-b) discernible at each site (=’species richness') to a number of biologically relevant covariates for which we had broad spatial coverage. The environmental covariates include depth and slope of the seafloor (Beaman et al. 2011), tidal current speed (Cougnon et al. 2013), floor current speed (Cougnon et al. 2013), surface productivity (Johnson et al. 2013, NASA Goddard Space Flight Center 2014) and the three key elements from our particle tracking models (i.e. arriving food-particles from the sinking-model, horizontal food flux, and settling food-particles from the settling-model).

Each transect was split at the boundaries of the environmental grid cells to ensure the pictures used to calculate average abundances and species richness all lay within the same value for the environmental covariates. A total number of 2685 images, distributed across 41 grid cells, were used in the analysis. Estimates of percent-cover of the broad functional groups were well distributed across the percent-cover-categories (Appendix A Fig. 9), therefore we treated the data as numeric. Using a weighted multiple linear regression, with weights allocated according to the number of pictures per environmental grid cell, allowed us to account for sampling effort and hence uncertainty in the estimated mean abundance of each sample. For the analysis of species richness, we included the logarithm of the number of images taken at each site as an offset in a negative binomial generalised linear model to account for an increase in species observed with increased sampling effort.

A model containing the main effects of all covariates was simplified by backward selection using AIC (Appendix A Table 2 & 4) and the stepAIC function from the MASS package. We then manually removed the non-significant term floor current speed ($F_{4, 36}$=22.67, p=0.179) from the model with the abundance of suspension feeders and the terms tidal current speed ($z_{4,35}$=1.87, p=0.061) and slope ($z_{3, 36}$=1.53, p=0.127) from the model with the richness of suspension feeders.

Suspension feeders are ecosystem engineers that promote species diversity by forming critical habitat for benthic communities. To test the relationship between cover of suspension feeders and the total number of benthic invertebrate species discernible at each site, we used a negative binomial generalised linear model and included the logarithm of the number of images taken at each site as an offset.

For the statistical analysis, we used R Version 3.2.0 (R Core Team 2016) and the packages 'raster' (Hijmans and 2015), 'MASS' (Venables and Ripley 2002) and 'mplot' (Tarr et al. 2015).

2.4.5 Data availability statement

Data that support the findings of this study are available from the Australian Antarctic Division under the identifier doi:10.4225/15/58742bff60898 (diatom abundances from surficial scrapes of the sediment grabs), and the identifier doi:10.4225/15/59dea9a19a61d (aggregated abundances and richness for all benthic groups).The particle tracking software is published as a R-package 'ptrackr' (Jansen and Sumner 2017), and available with the identifier doi:10.5281/zenodo.803493 or under www.github.com/janjansen86/ptrackr. All other relevant data are available from the corresponding author upon reasonable request.

2.5 Acknowledgements

We thank B. Raymond, S. Wotherspoon and S. Foster for their ideas and support in the analysis of the data, E. Cougnon for her help with the ROMS and S. Jansen and Jeroen Jansen for their help designing Fig. 2.1. C. Thun and B. Poignant (Geoscience Australia) prepared samples for the diatom analysis which was funded by a Joint US NSF East Asia and Pacific Summer Institutes and Australian Academy of Science Summer Fellowship at Macquarie University to J.P.W. C. Robineau (supported by Institut Polaire Français Paul Émile Victor (IPEV) and the Antarctic program IPEV 1124 REVOLTA) and J. Delaplanque-Lasserre (supported by Muséum national d'Histoire naturelle (MNHN) scored the benthic images. We thank the captain, crew and scientific party of the RV *Aurora Australis* who obtained the samples during the CEAMARC program as part of the IPY #53 Census of Antarctic Marine Life program, with particular thanks to G. Hosie (CEMARC program leader) and M. Riddle (chief scientist on board the RV *Aurora Australis*). Coastline and glacial features for the figures are taken from the Antarctic Digital Database version 5. J.J. is supported by a Tasmanian Graduate Research Scholarship and a QAS Top-Up scholarship. A.L.P. publishes with the permission of the Chief Executive Officer, Geoscience Australia. This work was completed as part of Australian Antarctic Science project 4124.

Chapter 3

Mapping Antarctic suspension feeder abundances and seafloor food-availability, and modelling their change after a major glacier calving

This chapter has been published as an article under the same title in
Frontiers in Ecology & Evolution **6**, 94 (2018)
doi: 10.3389/fevo.2018.00094

Jan Jansen[1,2], Nicole A. Hill[1], Piers K. Dunstan[3], Eva A. Cougnon[1], Benjamin K. Galton-Fenzi[2,4] & Craig R. Johnson[1]

[1] Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia
[2] Australian Antarctic Division, 203 Channel Highway, Kingston TAS 7050, Australia
[3] CSIRO Oceans and Atmosphere, 3-4 Castray Esplanade, Battery Point TAS 7004, Australia
[4] Antarctic Climate & Ecosystem Cooperative Research Centre (ACE CRC), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia

Abstract

Seafloor communities are a critical part of the unique and diverse Antarctic marine life. Processes at the ocean-surface can strongly influence the diversity and abundance of these communities, even when they live at hundreds of meters water depth. However, even though we understand the importance of this link, there are so far no quantitative spatial predictions on how seafloor communities will respond to changing conditions at the ocean surface.

Here, we map patterns in abundance of important habitat-forming suspension feeders on the seafloor in East Antarctica, and predict how these patterns change after a major disturbance in the icescape, caused by the calving of the Mertz Glacier Tongue. We use a purpose-built ocean model for the time-period before and after the calving of the Mertz-Glacier Tongue in 2010, data from satellites and a validated food-availability model to estimate changes in horizontal flux of food since the glacier calving. We then predict the post-calving distribution of suspension feeder abundances using the established relationships with the environmental variables, and changes in horizontal flux of food. Our resulting maps indicate strong increases in suspension feeder abundances close to the glacier calving site, fueled by increased food supply, while the remainder of the region maintains similar suspension feeder abundances despite a slight decrease in total food supply. The oceanographic setting of the entire region changes, with a shorter ice-free season, altered seafloor currents and changes in food-availability.

Our study provides important insight into the flow-on effects of a changing icescape on seafloor habitat and fauna in polar environments. Understanding these connections is important in the context of current and future effects of climate change, and the mapped predictions of the seafloor fauna as presented for the study region can be used as a decision-tool for planning potential marine protected areas, and for focusing future sampling and monitoring initiatives.

3.1 Introduction

Primary productivity is at the base of most marine ecosystems. In Antarctica, primary production is highly seasonal and intricately tied to the location, timing and duration of sea-ice and ice-free areas such as polynyas (Arrigo and van Dijken 2003). The collapse of large ice-shelves or calving of massive icebergs, and the retreat of sea-ice that is mainly observed around the Western Antarctic Peninsula in recent years (Parkinson and Cavalieri 2012), can dramatically alter the oceanographic setting with down-stream effects on the pattern of primary production hotspots and on Southern Ocean ecosystems (Arrigo et al. 2002, Gutt et al. 2011). Resulting changes in the location, timing and intensity of phytoplankton blooms (Cape et al. 2014) can influence the distribution of krill and predator aggregations (Gutt et al. 2011), the abundances of benthic suspension feeders (Fillinger et al. 2013, Gutt et al. 2013b) and can affect carbon storage (Peck et al. 2010).

For most seafloor communities living below the photic zone (~200 m), surface-derived primary production represents their main food source (Dayton and Oliver 1977, Duineveld et al. 2004, Ruhl et al. 2014), and is therefore critical for their survival. Seafloor communities represent the richest component of

Antarctic biodiversity (Griffiths 2010), are highly endemic (Griffiths et al. 2009), and play an important role in the marine ecosystem (Thurber et al. 2014). However, despite evidence that a changing environment influences the distribution of these communities (Gutt et al. 2011, Fillinger et al. 2013, Gutt et al. 2013b, Griffiths et al. 2017), no study has so far quantified and mapped how their distribution might change due to a changing icescape at the ocean surface. One of the reasons for the lack of quantitative studies is that although surface-derived food is one of the main drivers, it is only recently that the nature and strength of this relationship has been quantified on the Antarctic shelf using a so-called Food-Availability-Model (FAM) (Jansen et al. 2018c). Combining surface-productivity and ocean currents with particle-tracking, FAMs estimate the distribution of surface-derived food at the seafloor, and evaluate the estimates against data from sediment cores. Jansen et al. (2018c) demonstrated a strong link between modelled flux of suspended food along the seafloor and abundances of sessile suspension feeders, providing a framework that allows to estimate the distribution of key elements of the seafloor community and to predict how they may change with changing ocean productivity and currents.

One Antarctic region that has recently undergone drastic environmental changes is the George V shelf in East Antarctica. The calving of the Mertz Glacier Tongue (MGT) in 2010 (Young et al. 2010) has resulted in profound environmental changes in the region, such as increased sea-ice concentrations (Campagne et al. 2015), and changes in ocean currents along the shelf as suggested by observations (Aoki et al. 2017) and modeling studies (Cougnon et al. 2017, Kusahara et al. 2017). These environmental changes have consequences for the dynamics and distribution of primary production (Shadwick et al. 2013), the abundance of top-predators (Wilson et al. 2016), and has been observed to influence the community structure of shallow-water benthos (Clark et al. 2015). However, the effect of the MGT-calving on the seafloor across the region has so far neither been assessed nor observed, and so its impact on benthic communities across the continental shelf is still unknown. Obtaining this knowledge, however, is crucial for meaningful assessment of the comprehensiveness, effectiveness and representativeness of the proposed marine protected areas in this region.

Here, we (i) quantify differences in the environmental setting on the George V shelf that will affect the supply of food to the benthos. In our modelling, we apply a recently developed FAM (Jansen et al. 2018c) on two 5-year climatologies of remotely sensed surface chlorophyll-a for the period before and after the glacier calving, and use ocean current velocities from a purpose-built oceanographic model (Cougnon et al. 2017) (more details can be found in the Methods). We then (ii) map the distribution of benthic suspension feeder abundances before the glacier calving, using faunal abundances derived from underwater camera images and environmental predictor variables. Using the pre-calving statistical model for the suspension feeder abundances and the change in environmental conditions after the glacier calving, we then (iii) predict changes in suspension feeder abundances across the region, revealing the strong impact of the changing icescape on the seafloor ecosystem (Fig. 3.1 for general results, and Fig. 3.2 for an overview of the study-region).

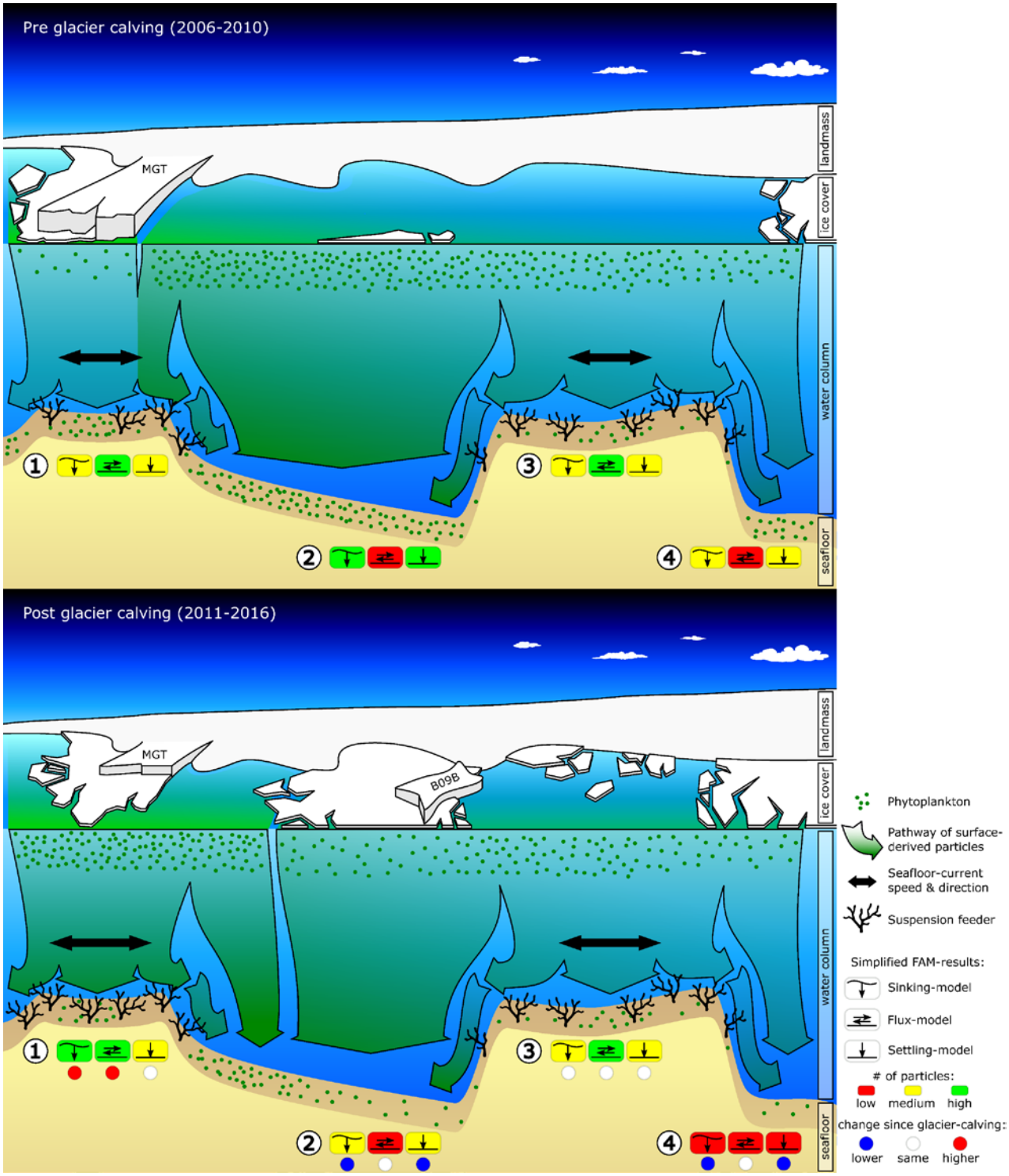


Figure 3.1: Graphic summarizing observed and predicted changes in environmental conditions (sea-ice, surface-chl-*a*, ocean current speeds, food-export) and seafloor fauna due to the calving of the Mertz Glacier Tongue (MGT) in 2010. The graphics shows a cross-section of the George V continental shelf approximately 80 km off the coast, looking South towards the Antarctic continent. The top graphic shows pre-calving environmental conditions and displays abundances of suspension feeders as observed from towed camera images. The bottom graphic shows observed changes in sea-ice, surface-chl-*a* and the position of the grounded iceberg B09B, as well as modelled changes in ocean current speeds, food-availability and suspension feeder abundances. Simplified food-availability-model (FAM) results are indicated for **(1)** Mertz Bank, **(2)** Adélie Sill, **(3)** Adélie Bank and **(4)** Adélie Basin. Additional indicators are included in the bottom graphic to highlight important changes.

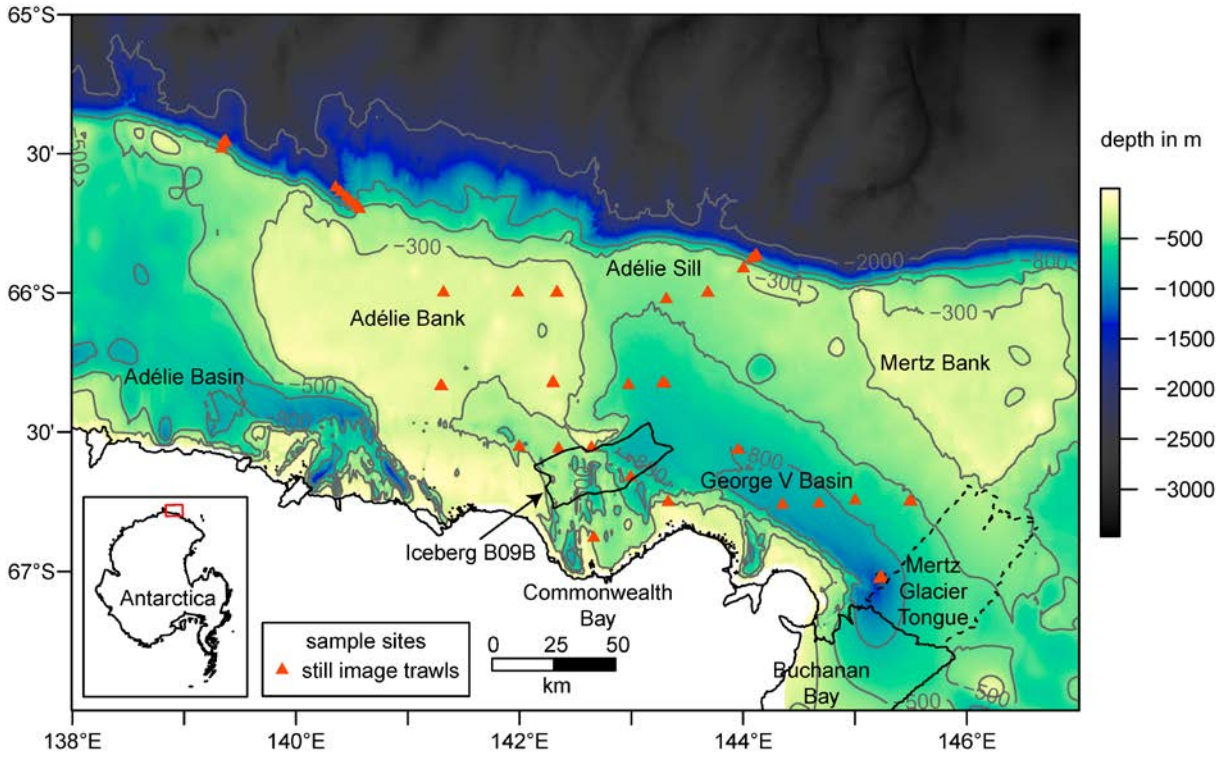


Figure 3.2: Bathymetry (Beaman et al. 2011) with selected contour lines (in grey), coastline and sample locations in the study area. Major glacial features such as the Iceberg B09B in the centre (location in 2016) and the Mertz Glacier Tongue (MGT) on the Eastern margin of the map are included. The dashed line shows the extent of the MGT prior to the calving in 2010. The inset map shows the location of the study area as highlighted by the red box.

3.2 Results

3.2.1 Changes in environmental conditions

Our results reveal that several aspects of the observed and the modelled marine environment have changed since the calving of the MGT (Fig. 3.3). Average sea-ice concentrations increased in the study region by 50-80%, particularly in the spring season, except over the Mertz Bank and where the calved MGT was located (Appendix B Fig. 1). Near the Mertz Bank, average surface-chlorophyll-*a* (chl-*a*) concentrations increase by a factor of two or more (Fig. 3.3c). The area of highest average surface-chl-*a* concentration also shows an eastward extension into areas previously covered by sea-ice. West of the Mertz Bank, the George V Basin and the Adélie Bank show decreasing values for surface-chl-*a* (Fig. 3.3c). In this area, the breakup of the sea-ice post-calving occurs much later in the year (Appendix B Fig. 1), shortening the time-period where surface phytoplankton is observed by satellites from around 4.5 months to 3 months. At the South-East tip of the Adélie Bank, north of the grounded giant iceberg B09B, the outline of a newly formed polynya (Tamura et al. 2012, Fogwill et al. 2016) can be observed, marked by lower spring-time sea-ice concentrations and higher surface-chl-*a* relative to the surrounding area. Modelled seafloor current speeds (Appendix B Fig. 2) increase by about 5 cm/s on the shallower sections of the shelf down to around 500m depth, and decrease by almost 50 % at the shelf break and slope, as well as in the area previously occupied by the MGT. Changing bottom tidal

current speeds account for almost all the increase in current speed on the South-Western flanks of the Adélie and Mertz Bank, in the deep George V Basin and below the iceberg B09B at the North-Western edge of Commonwealth Bay (Fig. 3.3f).

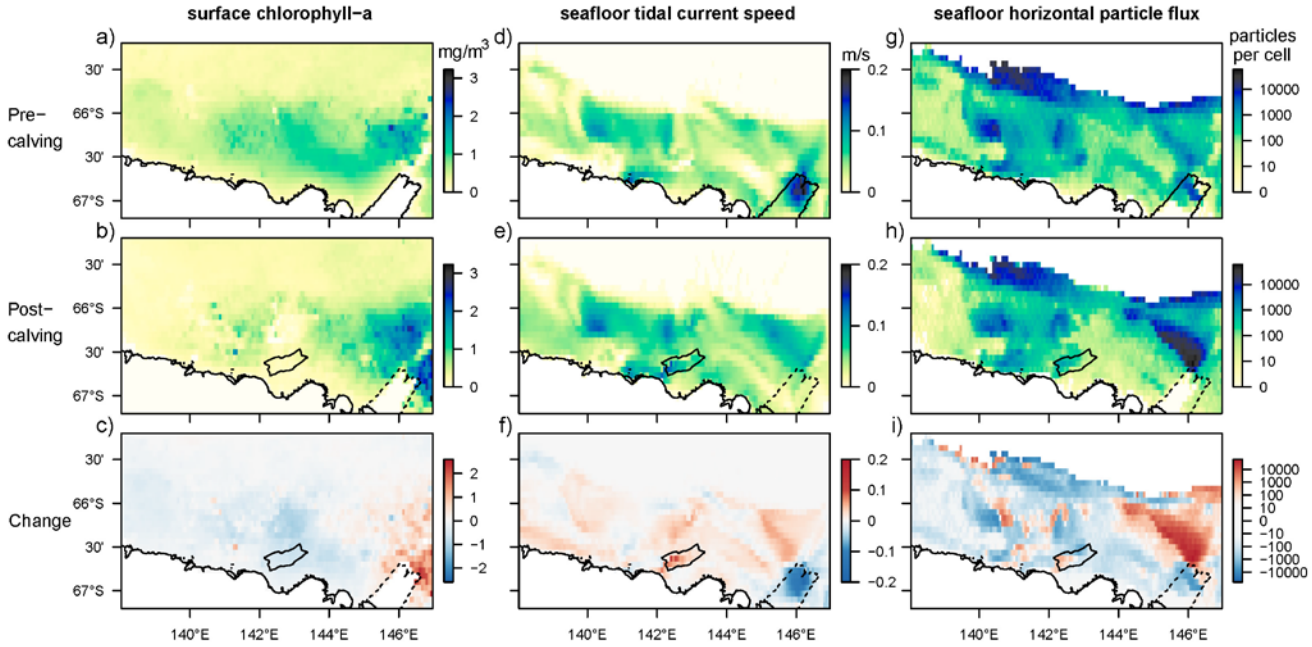


Figure 3.3: Comparison of mean values for selected biologically relevant environmental variables before and after the calving of the Mertz Glacier Tongue (MGT) in 2010. The first row shows environmental conditions in the five years leading up to the calving, the second row in the five years after, and the bottom row shows the magnitude of the change. **a**-**c**) are satellite-derived (MODIS-A) estimates of surface-chl-*a* corrected for Southern Ocean application (Johnson et al. 2013). The missing data at the previous location of the MGT stems from a landmask-artefact in the NASA-data. **d**-**f**) represent the speed of fluctuating currents (tidal currents) at the bottom layer of the regional ocean model used for this study (Cougnon et al. 2017). **g**-**i**) show the number of particles moving horizontally along the seafloor before their permanent sedimentation (on log-scale). In all maps the strongest changes can be observed in the Eastern section of the region, close to the location of the MGT. In the post-calving maps, the outline of the newly grounded iceberg B09B is added for reference while dotted lines indicate the original position of the glacier tongue before it broke off.

The Food-Availability-Model (FAM) tracks and quantifies three components of surface-derived food particles: the sinking component captures the advection of phytodetrital matter by currents as it sinks through the water column until it reaches the seafloor; the flux component represents the horizontal flux of food particles along the seafloor before sedimentation; the settling component represents the final location of advected particles after taking into account the redistribution by seafloor currents. Sinking and settling particles follow similar patterns to the other environmental variables mentioned before, with an eastward shift for the peak number of sinking and settling particles. The model-output shows an absence of sedimentation on large parts of the Mertz Bank (closest to the former tip of the MGT) due to increased current speeds (Appendix B Fig. 3). Horizontal food flux along the seafloor, which is dependent mainly on the interaction between the distribution of surface productivity and seafloor current speeds, increases 20-50 fold on wide sections of the Mertz Bank (Fig. 3.3i). In contrast, changes are more patchy on the Adélie Bank, where increases in flux are mostly restricted to the inner

section of the bank and the shelf break, while the edges of the bank experience decrease in flux. Further, most of the deeper sections of the shelf experience lower flux than before the calving.

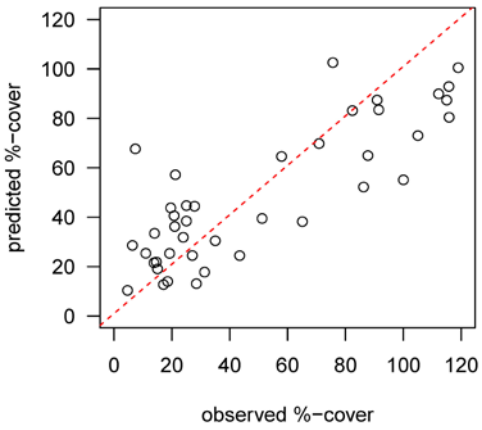


Figure 3.4: Diagnostic plot showing the fit between predicted values from the pre-calving statistical model and the observed %-cover estimates from benthic still images at the sample sites. The red dotted line indicates a perfect fit.

3.2.2 Predicted changes in suspension feeder abundances

Mapped predictions of suspension feeder (SF) cover are based on the statistical relationship between pre-calving cover estimated from still-images, and the environmental covariates depth and log (horizontal flux) (Appendix B Table 1, deviance-explained = 44 %), which are selected as the best predictor variables by the stepwise regression process (Appendix B Table 2). There is a good fit between the predicted values from the statistical model and the observed values at the sampling sites, with a slight underestimation of high cover values (Fig. 3.4). SF-cover before the calving is high on most of the shallower sections of the shelf (<500 m depth) (Fig. 3.5a), with values estimated between 60-100 % cover. The two shallow banks in the study area, the Mertz Bank closest to the MGT in the East and Adélie Bank in the West, show relatively similar patterns of SF-cover, with average values of around 60 % except for on the edges of the banks, where cover of suspension feeders may reach up to 100 %. In contrast, post-calving predictions show a clear difference between the two banks (Fig. 3.5b) in that SF-cover is predicted to increase by 20-40 % (Fig. 3.5c) on large parts of the Mertz Bank, while the Adélie Bank and other areas retain similar SF-cover as previously. The strong predicted increase in SF-abundance on the Mertz Bank in the east stems directly from the 20-50-fold increase in predicted particle flux that is a direct result of both increased surface production and stronger tidal currents.

3.3 Discussion

We predict that the calving of massive icebergs will have far-reaching effects on benthic communities mediated through the mechanism of pelagic-benthic coupling, and that changes occur even hundreds of kilometers away from the glacier tongue. While previous studies have shown that calving events can have localized negative impacts on the benthos through iceberg scouring (Gutt et al. 1996), here we predict that the combination of changes in local oceanography and surface production influences patterns of seafloor food-availability at much larger scales. Particularly strong changes are predicted

in the horizontal flux of food particles post-calving, which is important in determining the distribution of suspension feeders (Jansen et al. 2018c). Similar to other Antarctic regions that have recently become ice-free (e.g. Fillinger et al. 2013), our results suggest environmental conditions on the Mertz Bank now are much more favorable for suspension feeders (SFs) than before the calving. Our modelling suggests that there will be a strong, but locally confined increase in SF-abundance on the Mertz Bank of up to 40 %. Further away, near the Adélie Bank, increases in bottom current speeds seem to compensate for the overall decrease in food supply, resulting in a prediction of only marginal changes in SF-abundance. The distribution of surface production around the newly formed polynya on the leeward side of the grounded iceberg B09B (Fogwill et al. 2016) seems to slightly influence SF-abundances with relatively stable cover predicted beneath the polynya in contrast to decreasing cover in the ice-covered area directly north of the iceberg B09B. Close to and below the position of the tip of the MGT before it broke away, where Beaman and Harris (2005) have previously found a high number of macrobenthic species, including many sponges and bryozoans, our model predicts a substantial decrease in SF-abundance, due to a decrease in floor current speed affecting the horizontal food-flux. However, we caution that little confidence should be placed in this result; the environmental conditions in this area might be unique due to the glacier tongue and we lack biological samples for this area. Further, we also lack confidence in the food-availability-data because of missing data in the remotely sensed surface chl-*a* dataset (see Methods section 4.2.2). Unfortunately, the shallower sections of the Mertz Bank and the western part of the Adélie Bank, which we show here are particularly interesting areas, have not been physically sampled as part of the survey (see Fig. 3.2). However, because the survey was designed to cover a wide range of depths and geomorphologies (Hosie et al. 2011), because of the high confidence in the predicted values from the statistical model (Fig. 3.4), and because of the similarity in environmental conditions between the shallow banks prior to the glacier calving, we are confident the relationship between environmental variables and distributional patterns of suspension feeder abundances is consistent across the region.

Regions around ice-shelves and glacier tongues provide valuable insight into the dynamic environment of the Antarctic shelf. When an ice-shelf calves a massive iceberg or collapses entirely, the marine environment, to which species might have acclimated to for many years, can transition quickly between a food-poor and a food-rich system (Gutt et al. 2011). The MGT is thought to calve massive icebergs in a ~70 year cycle (Campagne et al. 2015, Giles 2017), meaning that there are likely also differences in the long-term stability of environmental conditions, and in the frequency of iceberg-scour between the Mertz Bank near the MGT and the Adélie Bank in the West of the George V shelf. Studies on the West Antarctic Peninsula suggest that at least some components of Antarctic benthic communities on the shelf, such as glass sponges and pioneering species, can increase rapidly in areas that are newly ice-free, fueled by higher export of surface production (Gutt et al. 2011, Fillinger et al. 2013). Conversely, slower-growing deep-sea corals and bryozoans may respond more slowly to changing environmental conditions. Whether any species or communities have adapted to these long-term cyclic events in the George V region is unknown, because a comparative study between the Mertz and Adélie Bank has so far not been conducted due to a lack of biological data. Further, it is currently also not possible to validate our predictions with independent data, because there have been no comprehensive observations of the deep seafloor since the glacier calving. However, if the benthic community

response in East Antarctica is similar to that of the West Antarctic Peninsula, the community composition on the Mertz Bank can be expected to change rapidly in the more favorable environment after the glacier calving, or will have undergone changes already, given that eight years have passed since the calving event. The postulated more favorable environment on the Mertz Bank might continue to persist for some time until the MGT regrows the ice tongue. Further, oceanographic models from after the calving indicate an increase in basal melting of the MGT due to warmer, faster moving waters from the east after grounded tabular iceberg relocation and the MGT calving (Cougnon et al. 2017) which may slow the regrowth of the MGT.

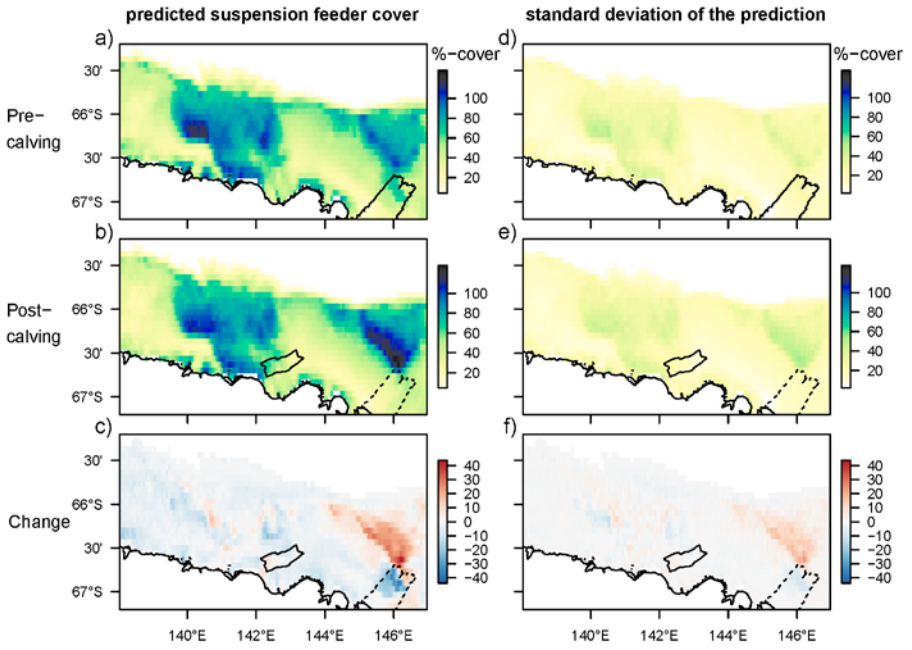


Figure 3.5: Spatial predictions of percentage cover of suspension feeders on the seafloor before and after the glacier calving. The cover of each species is estimated separately, thus overlapping cover can result in total coverage exceeding 100 %. **a**-**c**) show the predicted mean, and **d**-**f**) the standard deviation of the predictions. Note that changes are most pronounced on the Mertz bank close to where the glacier calving happened. The high predicted cover pre-calving under the glacier tip is driven by high current speeds, but samples have so far not been taken in this location.

Food-availability is a key factor influencing species distributions. Here, we map predicted changes in relevant seafloor-food-availability caused by the calving of a major glacier tongue, and predict change in distributional patterns of benthic suspension feeders, a key element of Antarctic biodiversity. The study area on the George V shelf lies within the recently proposed East Antarctic MPA (AAD 2017), and we suggest the Mertz Bank and Adélie Bank should be considered as distinct areas for future sampling of the benthic community. The predicted distribution of suspension feeders after the glacier-calving provides an up to date picture of a key part of seafloor biodiversity, from which the representativeness of the proposed MPA can be assessed. Until regular monitoring programs are established, modelling studies such as ours give important information and context for future monitoring and assessment. Our study provides insight into temporal change and into the mechanisms that drive changes at the seafloor. This is important for a holistic understanding of the Antarctic marine ecosystem, and helps us to understand how climate change can affect the seafloor in the future.

3.4 Methods

3.4.1 Study area

The study area is located on the relatively deep (500-700 m) East Antarctic continental shelf and slope between latitudes 139°E and 147°E (Fig. 3.2). The depth of the shelf ranges between 200 m on the banks to 1300 m in the basins. The most prominent feature in this region is the Mertz Glacier Tongue (MGT) in the east which has strong influences on both oceanography (Barber and Massom 2007) and biology(Arrigo and van Dijken 2003, Sambrotto et al. 2003, Beans et al. 2008, Jansen et al. 2018c). Strong katabatic winds in the region drive sea-ice production (Massom et al. 2001), convection of dense water that contributes to overturning circulation (e.g. Williams et al. 2008), and importantly also form ice-free surface areas on the westward sides of the MGT and the grounded icebergs. These permanent ice-free areas support a long growing season for phytoplankton resulting in high phytoplankton productivity (Arrigo and van Dijken 2003, Sambrotto et al. 2003, Beans et al. 2008). Abundant and diverse benthic suspension feeder communities have been found primarily on the shallower section of the shelf between 200-600 m (Post et al. 2011). Further, tidal currents on the seafloor redistribute surface derived production, with flux rates of organic particles directly related to the abundance and species richness of the benthic community (Jansen et al. 2018c).

The MGT calves off massive icebergs in an estimated 70-year cycle (Campagne et al. 2015), the last event happening in 2010 after a collision between the massive iceberg B09B and the MGT. Since the calving of the MGT, the Mertz Polynya has decreased significantly in size (Tamura et al. 2016), changing ocean circulation (Aoki et al. 2017, Cougnon et al. 2017, Kusahara et al. 2017) and increasing sea-ice concentrations (Tamura et al. 2012). The iceberg B09B grounded on the South-Eastern flank of the Adélie Bank shortly after the collision, and a new polynya has formed on its leeward side (Fogwill et al. 2016). For more details on the study area and the oceanography we refer to numerous papers on the region (e.g.Beaman and Harris 2005, Cougnon et al. 2013, Shadwick et al. 2013, Cougnon et al. 2017, Kusahara et al. 2017, Jansen et al. 2018c).

3.4.2 Environmental data and numerical modelling

3.4.2-a Ocean model and bathymetry

Ocean current speeds and directions before and after the glacier calving are derived from a tide-simulating oceanographic model for the George V shelf developed by Cougnon et al. (2017) based on the Regional Ocean Modelling System (ROMS) (Shchepetkin and McWilliams 2005). The model setup used here is similar to that described by Cougnon et al. (2013), using the same horizontal and vertical grid. The horizontal grid has a resolution of 2.16 km near the southern boundary and 2.88 km near the northern boundary. The vertical grid is arranged to give higher resolution at the top and bottom of the water column. The model domain encompassed the area from the Antarctic coastline to the deep ocean at 62.72°S, and from 135.77°E to the west of the French base, Dumont D'Urville, to 158.08°E to the east of George V Land (Cougnon et al. 2013).

The model includes ocean-ice shelf thermodynamics described by three equations following Holland and Jenkins (1999), frazil ice thermodynamics following Galton-Fenzi et al. (2012a), as used in previous studies (e.g.Cougnon et al. 2013, Gwyther et al. 2014) and a simplified analytic tidal forcing at the

lateral boundaries (Cougnon et al. 2017 for details). The bathymetry in both simulations is based on RTopo-1 (Timmermann et al. 2010), and modified to include local high-resolution bathymetry (Beaman et al. 2011) as described in Mayet et al. (2013). Ice draft of the MGT and B09B, along with the underlying bathymetry, is based on an early version of the most up-to-date product by Mayet et al. (2013).

The total run time of the model for each simulation(before and after calving) is 33 years, using an annually repeating loop of the same lateral forcing for both simulations and an annually repeating loop of the surface forcing corresponding to each icescape. This 33 year run includes a spin-up phase of 30 years to reach equilibrium. The spin-up phase of the model has no relevance for the seafloor communities, but is a procedure to ensure the ocean model reaches equilibrium (so that the ocean heat content and the ocean currents are relatively stable under the applied forcing, allowing to analyze the output). The iceberg B09B is at equilibrium in the model. In the model, icebergs and ice-shelves are steady and do not move or change shape. However, they are thermodynamically active, which means that heat and salt fluxes due to ocean-driven melting/refreezing are taken in consideration.

3.4.2-b Surface productivity and sea-ice

We estimated spatial patterns of surface productivity from measures of ocean colour derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua) (NASA Goddard Space Flight Center 2014). We used Level-3 binned daily remote sensing reflectance, provided at a resolution of 4km equal-area bins, and corrected the values for Southern Ocean application using the algorithm in Johnson et al. (2013). Daily measures of chlorophyll-a concentrations were averaged for southern hemisphere spring and summer in each year for a five-year period before (2005-2009) and after (2011-2016) the calving of the MGT. There are no data available from NASA for the area previously covered by the MGT, presumably due to a landmask artefact.

We estimated seasonal patterns of sea-ice concentrations from satellite-measures of Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data (Cavalieri et al. 1996 , updated yearly). Daily measures of sea-ice concentrations were averaged for southern hemisphere spring and summer in each year for a five-year period both before (2005-2009) and after (2011-2016) the calving of the MGT.

3.4.2-c Food availability model (FAM)

We mapped the availability of surface-derived food at the seafloor before and after the calving event using a validated food-availability model (FAM) as described in Jansen et al. (2018c). The FAM uses a distribution of particles that is based on multi-year averages of satellite derived chlorophyll-a (section 4.2.2), and tracks individual particles from the surface to the seafloor while accounting for their sinking speed, the speed and direction of currents (section 4.2.1) in 3D, and the sedimentation-rate of particles on the seafloor based on particle sizes (Jansen et al. 2018c). The model generates three maps of food availability, namely a sinking-map (showing the number of particles arriving/temporarily settling on the seafloor), a map of horizontal flux (showing where particles move along the seafloor before their sedimentation), and a settling-map (showing where particles permanently settle on the seafloor). While the objectives in our study differ strongly from the Jansen et al. (2018c)-study (Jansen et al. described & validated a new method, while we apply the method to map the distribution of suspension feeders and their changes through time), the only difference in the food-availability model is using a different ocean model and a different surface-chl-*a* climatology. Current speeds on the shelf seem to be slightly

lower in the pre-calving part of the model developed by Cougnon et al. (2017) compared to that of Cougnon et al. (2013), but are within the seasonal variation of the Cougnon et al. (2013) model.

For the particle tracking, we used four consecutive time-slices of the ocean-model for the summer season before and after the calving respectively. We used the four consecutive time slices with the strongest differences in current direction and speed, to ensure that each time slice adequately captures one full tidal movement (a 6h time-slice with 3 hours of incoming tide and 3 hours of outgoing tide would show very little current speed). The maximum number of seed particles was ~4.5 million for the pre-calving model and the particles were tracked in 30 min time-steps. At each time-step the location of each particle with respect to the ROMS-cells was calculated, and water current speed and direction at that location updates for advection of the particles during the next time-step. Particles were stopped when they either moved out of the study area or matched the stopping criteria for the respective model, as described in Jansen et al. (2018c). The resulting particle distributions from each model-run were back-transformed into a regular grid with a resolution of 1/15 degrees.

We use the FAM-parameters previously defined for this region (Jansen et al. 2018c), namely a sinking speed of 300 m/day, a particle radius of 0.24 mm, the density of seawater at 1030 kg/m^3, the density of settling particles at 1100 kg/m^3 and an aspect ratio of 1 representing idealised spherical particles in our modelling.

For the particle tracking, we used R Version 3.3.1 (R Core Team 2016) with the packages 'ptrackr' (Jansen and Sumner 2017), 'raster' (Hijmans and 2015), 'ncdf4' (Pierce and 2014), 'nabor' (Elseberg et al. 2012), 'geostatspat' (Brown 2015) and 'spatstat' (Baddeley and Turner 2005).

3.4.3 Biological data collection

We use the same dataset of benthic images as used by Jansen et al. (2018c), which is available through the Australian Antarctic Division Data Centre (Jansen et al. 2017). It comprises detailed underwater still images collected during the Collaborative East Antarctic Marine Census (CEAMARC) for the Census of Antarctic Marine Life in December 2007 to February 2008 (Hosie et al. 2011). Transects during the CEAMARC were designed to cover a wide range of depths and geomorphologies in the region and therefore can be considered representative of the area modelled. A forward facing 8 megapixel Canon EOS 20D SLR with two speedlight strobes was mounted on a beam trawl and pictures were taken every 10 seconds. 32 sites were sampled with transect length mostly between 4-6 km, with exceptions ranging between 3-16 km. The trawl was controlled using a deck winch. Benthic fauna were identified to the lowest taxonomic resolution possible and, where species identification was not possible, specimens with similar overall appearance were grouped into morphotypes. The bottom third of each image was scored. For each image, the abundance of each species/morphotype was estimated within 5% bins from 0% to 50% and 10% bins from 50% to 100%. Using taxonomy and body-type along with expert knowledge, the abundance of the suspension feeding fauna in each picture was calculated.

3.4.4 Statistical Analysis

We use the image data and the maps of environmental data for 2005-2009 to generate a pre-calving statistical model, aiming at producing the statistical model that best explains the abundance of

suspension feeders (SF). Each transect was split at the boundaries of the environmental grid cells to ensure all pictures lay within the same value for the environmental covariates. We multiplied %-cover estimates in each image by 100 and rounded up to generate integer values that better suit a statistical analysis using a multiple linear regression with a negative binomial GLM (assuming the values would then represent the number of pixels covered by the fauna). We backwards selected variables from a full model using AIC. The full model contained the important environmental variables identified by Jansen et al. (2018c), namely depth, tidal-current speed and the horizontal flux of particles along the seafloor. The final model contained only depth and log(horizontal-flux) as predictor variables. We found that using a negative binomial generalized linear model (compared to a linear model in the previous study) did not affect the selection of model terms. Therefore, the change in selected model terms is likely to come from the difference in the ocean model or the surface productivity. The pre-calving statistical model showed a good fit between the predicted and the observed values at the sample sites, with possibly a slight underestimation of suspension feeders at high abundances (Fig. 3.5). Due to the limited amount of biological data available, we were not able to use separate datasets for training and testing the statistical model.

We then used the pre-calving statistical model to predict the spatial distribution of SF-cover in both the pre-calving and the post-calving environment. The difference between the resulting maps was used to make inferences about areas with expected increases and decreases in the abundance of suspension feeders. Further, we bootstrapped the parameters of the pre-calving statistical model to obtain estimates for the standard-deviation of the predictions.

For the statistical analysis, we used R Version 3.3.1 (R Core Team 2016) and the packages 'raster' (Hijmans and 2015), 'MASS' (Venables and Ripley 2002), 'maptools' and 'modEvA'.

3.4.5 Data availability

Estimates of suspension feeder abundances from benthic images are available through the Australian Antarctic Division Data Centre (Jansen et al. 2017). Raster files containing mapped predictions of food-availability and suspension feeder abundances presented in this study, from before and after the glacier calving are available through the Australian Antarctic Data Centre (Jansen 2018).

3.5 Acknowledgements

We thank Marc Eléaume for useful discussions and for making the original biological data available to us. Biological samples were collected during the CEAMARC program as part of the IPY #53 Census of Antarctic Marine Life program. Coastline and glacial features for the figures are taken from the Antarctic Digital Database version 5. J.J. is supported by a Tasmanian Graduate Research Scholarship and a QAS Top-Up scholarship. This work was completed as part of Australian Antarctic Science project 4124.

Chapter 4

Taxonomic resolution, functional traits, and the influence of species groupings on mapping Antarctic seafloor biodiversity

This chapter has been published as an article under the same title in
Frontiers in Ecology & Evolution **6**, 81 (2018)
doi: 10.3389/fevo.2018.00081

Jan Jansen[1,2], Nicole A. Hill[1], Piers K. Dunstan[3], Marc P. Eléaume[4] & Craig R. Johnson[1]

[1] Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia
[2] Australian Antarctic Division, 203 Channel Highway, Kingston TAS 7050, Australia
[3] CSIRO Oceans and Atmosphere, 3-4 Castray Esplanade, Battery Point TAS 7004, Australia
[4] Muséum National d'Histoire Naturelle, UMR 7205-ISYEB, MNHN-CNRS-UPMC-EPHE, 57 Rue Cuvier, CP51, 75231, Paris Cedex 05, France

Abstract

Benthic marine biodiversity on the Antarctic continental shelf is high and unique, yet its distributional patterns are still relatively poorly understood. Some of the main issues are that biological data are sparse, and that many species are rare and seem only weakly related to environmental conditions. Grouping species by taxonomic or functional similarity has historically been used to compensate for missing species identification, to generate a more widespread distribution of data-points, and this practice can help to gain a better understanding of the distribution of biodiversity. However, there are few guidelines on how to group species, the implicit assumptions about species associations in the groups are difficult to validate, and the information loss associated with grouping species is unknown.

Here, we analyse whether grouping benthic macrofaunal species by taxonomic or functional similarity preserves distributional patterns seen in species distributions, using a model-based approach called 'species archetype model' that groups species or other units based on the similarity in their responses to environmental factors. Using presence-absence data, the species archetype models identify twice as many assemblages when used on the highest taxonomic resolution data, than when applied to taxonomic data at lower resolution (e.g. class) or functional groups based on mobility, feeding type and body shape. Further, confidence in the predictions of either taxonomic or functional groups is far less than for predictions based on the highest taxonomic resolution data. Although using functional groups is often thought to accumulate species with similar environmental responses, our analysis shows that functional groups may insufficiently resolve assemblage structure for presence-absence data. Model-based approaches provide key information to understanding the regional distribution of Antarctic marine biodiversity, and care needs to be taken when using a-priori groupings of species to make statements about the distribution of biodiversity.

4.1 Introduction

The ocean surrounding the Antarctic continent supports unique assemblages of highly diverse benthic marine species (Griffiths et al. 2009, De Broyer et al. 2014, Chown et al. 2015). However, the remoteness which has protected this pristine environment for a long time also means that biological data for the region are sparse (De Broyer et al. 2014). Sparse biological data, the rarity of many Antarctic species, limited environmental predictor variables (Jansen et al. 2018c) and inconsistent relationships between biological data and environmental conditions across the regions and taxa studied (Cummings et al. 2010, Convey et al. 2014) are all reasons that the distributional patterns of seafloor biodiversity around Antarctica are still relatively poorly understood (Brandt et al. 2007, Chown et al. 2015). This is an issue because lack of knowledge about the distribution of biodiversity hinders (1) informed marine spatial planning in Antarctica, including the implementation of conservation measures, (2) policy development underpinning regulation of human activity in Antarctica, and (3) predicting the response of Antarctic marine ecosystems to environmental change.

Statistical models that link the occurrence of biota with relevant environmental factors are one way of making the most of sparse biological data to understand and map the distribution of benthic communities and their biodiversity. To date efforts to map seafloor communities have either focused

on a few common species of echinoids (Gutt et al. 2012, Pierrat et al. 2012), or have been based on dissimilarity metrics (Koubbi et al. 2011a), expert opinion (Gutt et al. 2013c), or aggregating species with functional similarity (Jansen et al. 2018a). However, while these efforts provide useful insight into the distribution of biodiversity, they either analyse only a single component of the benthic community, they lack reproducibility, or individual species responses are difficult to identify (in the case of multivariate distance based approaches).

Aggregating species by taxonomic or functional similarity is a common approach to overcome difficulties in analysis of data with many rare species (e.g. Cunningham and Lindenmayer 2005, Rooper et al. 2014, Jansen et al. 2018a), that comprise a substantial number of the species in any community. Traditionally, species are often grouped by their taxonomy, further motivated by constraints in time, expertise, or funding. More recently, species have been aggregated or classified according to functional traits. Functional traits define a species in terms of their ecological role and can include body size, other morphological characteristics and life history traits. Further, these traits are thought to be related to the performance of a species, and therefore its occurrence and abundance, under particular environmental conditions (Webb et al. 2010). In grouping species based on functional traits, it is assumed that different species with common functional traits respond to environmental gradients in a similar way. Because this approach provides a more mechanistic understanding of the structure and function of assemblages and their response to change (Sunday et al. 2015a), it has attracted much interest (Petchey and Gaston 2006, Cadotte et al. 2015). In Antarctica, functional traits such as mobility and feeding-strategy have been described as important factors influencing species distributions, with species commonly classified into mobile deposit feeders and sessile suspension feeders (e.g. Barry et al. 2003, Jansen et al. 2018c). While sessile suspension feeders, such as Bryozoans, Corals and Sponges are often associated with steep slope habitats and rocky substrate, mobile deposit feeders such as Holothurians and a range of burying fauna inhabit softer sediments in areas with low current speeds (Barry et al. 2003). Functional approaches can result in spatial patterns that are distinctly different to those based on traditional taxonomy and inform us about how communities are structured (Stuart-Smith et al. 2013). However, there are few guidelines on *how* and at which *level* to group species, yielding a wide variety of approaches that are dependent on individual researchers. Further, the assumptions about species associations in the groups are difficult to validate and it is unknown how much information about biodiversity patterns is lost when species are grouped.

In contrast to a-priori groupings, model-based approaches, such as Species Archetype Models (SAMs)(Dunstan et al. 2011), allow grouping species or other units based solely on the similarity of their response to a suite of environmental covariates. SAMs are based on generalised linear models, are defined for a range of different types of data, and importantly for our context are able to model rarer species. Also, because SAMs are purely based on environmental responses, the resulting archetypes are not a result of any a-priori assumptions about species associations. Model-based approaches are a relatively new statistical tool, but have already shown promising results for mapping species and habitat distributions (e.g. Woolley et al. 2013, Hill et al. 2017, Ovaskainen et al. 2017).

In this study, we use SAMs to map the benthic invertebrate community on the George V shelf in East Antarctica. We use presence-absence data from underwater camera images in which taxa have been

identified to the highest taxonomic resolution possible, and use two additional versions of the same dataset in which species were grouped a-priori by taxonomic or functional similarity. We hypothesise that species with similar functional traits in mobility, feeding-type and body-shape respond in a similar way to environmental conditions, and that grouping species before analysis only marginally affects predicted biodiversity patterns. Further, we hypothesise taxonomic groupings of species aggregate different functional traits, and therefore expect predicted biodiversity patterns to differ from both the analysis of functional group and of the species-data, unless niche-conservatisms is high in which case an analysis of taxonomic groups would differ only little from patterns observed in the species-data.

4.2 Methods

4.2.1 Study area

The study area is the George V continental shelf and slope in East Antarctica, spanning latitudes 139°E to 147°E from the Antarctic coastline to the shelf break at around 65.5°S. Water depth on the shelf is typically 500-700 m, punctuated by bathymetric features including the Mertz and Adélie Banks (200-250 m depth) and the George V and Adélie Basins (depths up to 1300 m) (Fig. 4.1). The oceanography in this area is mainly influenced by the Mertz Glacier Tongue and the adjacent Mertz Polynya (Cougnon et al. 2013), an area of ice free water that drives water circulation (Massom et al. 2001) and supports a relatively long growing season of phytoplankton (Sambrotto et al. 2003, Beans et al. 2008). Abundant and diverse benthic communities have been found primarily on the shallower section of the shelf between 200-600 m and on the shelf break (Post et al. 2011), and modelling work suggests widespread cover of suspension feeders on the banks (Jansen et al. 2018a).

4.2.2 Biological data

4.2.2-a Data collection and scoring

Biological data were collected during the Collaborative East Antarctic Marine Census (CEAMARC) for the Census of Antarctic Marine Life in December 2007 to February 2008 (Hosie et al. 2011).

Detailed underwater still images were obtained from a forward facing 8 megapixel Canon EOS 20D SLR with two speedlight strobes mounted on a beam trawl. Transects at 32 sites were mostly 4-6 km long (with some exceptions ranging between 3-16 km) and the water depth at the sample sites was between 200 m and 1550 m. The trawl was controlled using a deck winch and pictures were taken every 10 seconds. Fauna were identified to the lowest taxonomic resolution possible. Where species identification was not possible, specimens with similar overall appearance were grouped into morphotypes (operational taxonomic units, or OTU). The bottom third of each image was scored. For each image, the abundance of each OTU was estimated within 5 % bins from 0 % to 50 %, and 10 % bins from 50 % to 100 %. Although abundance was recorded from the images, the statistical method we used required reducing the data to presence-absence for analysis (see section 4.2.4). The image-derived data from each transect was then split at the boundaries of the environmental grid cells to ensure pictures used in the analysis all lay within the same value for the environmental covariates. A total number of 2685 images, distributed across 41 grid cells, were used in the analysis.

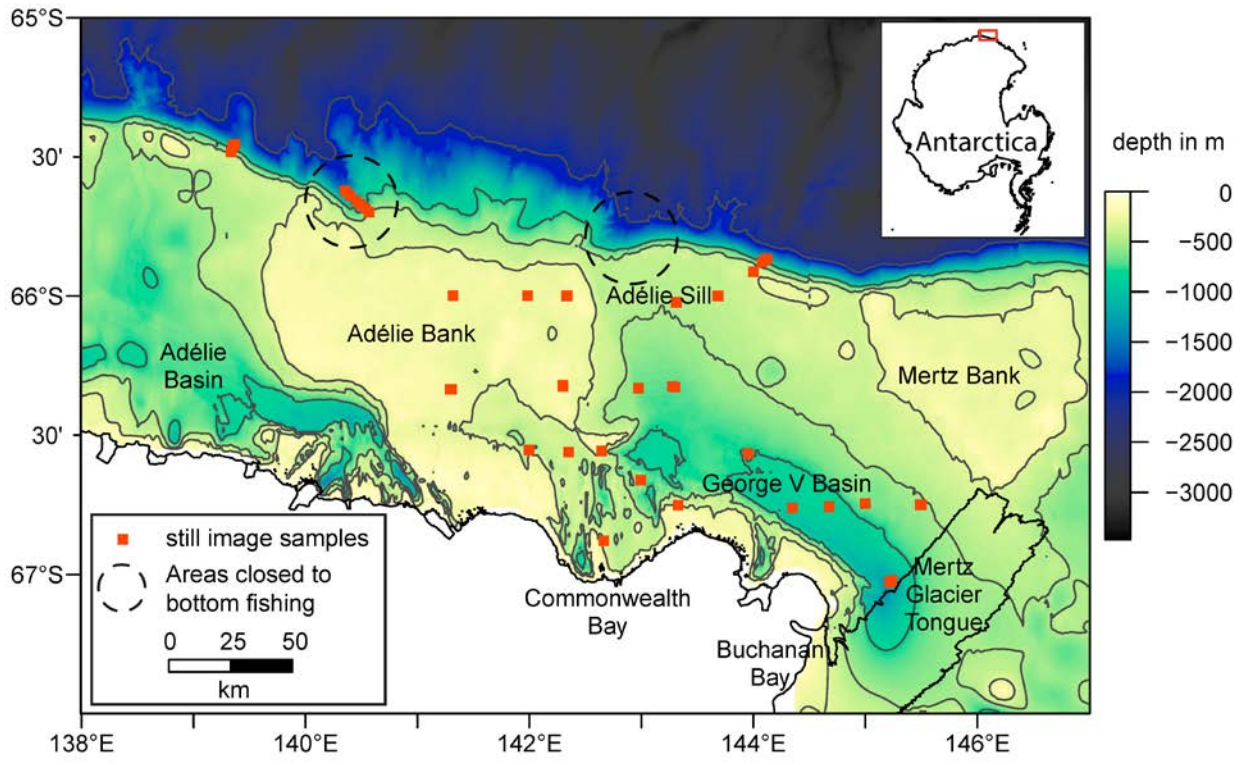


Figure 4.1: Overview of the George V shelf, East Antarctica. Shown are the bathymetry (Beaman et al. 2011) with selected contour lines (in grey), coastline, sample locations and approximate location of areas closed to bottom fishing due to the presence of vulnerable marine ecosystems (Jones 2017). The inset map in the top right corner shows the location of the study area as highlighted by the red box.

4.2.2-b Functional and taxonomic groupings

From the raw dataset comprised of 172 OTUs (Appendix C Table 1), we generated two aggregated datasets using expert knowledge. One dataset comprised OTUs grouped purely by taxonomy, and the other with OTUs grouped by functional traits. Each OTU was identified to the highest taxonomic resolution possible, and for each OTU we defined its mobility (mobile or sessile), its feeding-type (deposit feeders, opportunists, predators, active and passive suspension feeders), and body shape (12 categories). We chose these three categories of functional traits because they can be identified from images and expert knowledge, and because Antarctic benthic communities have been categorised in a similar way in the past, although not in such detail (Gutt et al. 2013c). By aggregating OTUs with the same combination of these three functional traits, we identified 30 different functional groups (the full range of functional groups is listed in Appendix C Table 2).

Taxonomic grouping was done mostly at the class and phylum level. As a general rule, we aimed at creating a number of taxonomic groups similar to the number of functional groups to aid comparison. On average five OTUs were grouped together to form a taxonomic group, although in seven instances only a single OTU represented an isolated taxonomic group. In total, we identified 27 taxonomic groups (Appendix C Table 3).

4.2.3 Environmental data

The environmental covariates used for model predictions were those that are commonly considered important for describing the habitat of benthic invertebrates. They were depth, slope of the seafloor and topographic position index derived from Beaman et al. (2011), ocean current speed, tidal current speed and temperature at the seafloor derived from an oceanographic model (Cougnon et al. 2013), and three measures for the availability of food at the seafloor from Jansen et al. (2018c) (i.e. food-particles arriving near the seafloor after sinking from the surface, horizontal flux of food along the seafloor, and food-particles settling onto the seafloor). We did not include other environmental covariates because of their high correlation with variables already selected, namely surface productivity (highly correlated with the number of sinking particles arriving near the seafloor; Pearson's r = 0.971), and roughness of the seafloor (highly correlated with slope; Pearson's r = 0.992). In the map of the settling particles, 35 out of 2515 grid-cells contained exceptionally high values, ranging from 1035 – 5122. These values are likely an artefact of the modelling process rather than a pattern likely to be observed, and we therefore arbitrarily adjusted the values those cells to 1000 particles.

4.2.4 Statistical analysis

Data were analysed using species archetype models (SAMs) (Dunstan et al. 2011), which are based on generalised linear models and define groups of taxa based on their similar responses to environmental covariates. These groups are termed 'species archetypes'. Currently, SAMs are developed only for presence-absence data and count-data, and we therefore reduced our raw-dataset from percent-cover estimates to presence-absence for the SAM-analysis. For the boxplots presented in Fig. 4.2 and Fig. 4.5, we used the percentage-cover estimates for individual OTUs in the respective species archetypes to aid interpretation of the results. For the SAM-analysis, we considered all of the environmental covariates in section 4.2.3 and included a polynomial term for depth and the logarithm for slope. We used Bayesian information criteria (BIC) for selecting the optimal number of species archetypes in each of the three datasets (OTUs, taxonomic groups and functional groups), running 50-iterations of the same model with random starts and extracting the BIC in each of these models to ensure that inference was based on the global maximum of the likelihood-surface. The model with the optimal number of species archetypes as determined by BIC (see Appendix C Fig. 1 for the OTU-analysis) was then used to predict the occurrence of the species archetypes across the study area. This prediction uses the relationship identified between species archetypes and the environmental covariates, and then predicts species archetype occurrence in areas where only environmental data are available. We restricted the prediction area to the continental shelf down to ~1500m depth, the maximum depth that the camera was deployed.

For the statistical analysis, we used R version 3.3.1(R Core Team 2016), and the SAMs were developed using the R package 'SpeciesMix' (Dunstan et al. 2011).

4.2.5 Data availability

The full biological dataset is published in Robineau et al. (2018) and is publically available through the Australian Antarctic Division (doi:10.4225/15/5ae7cf565cebb).

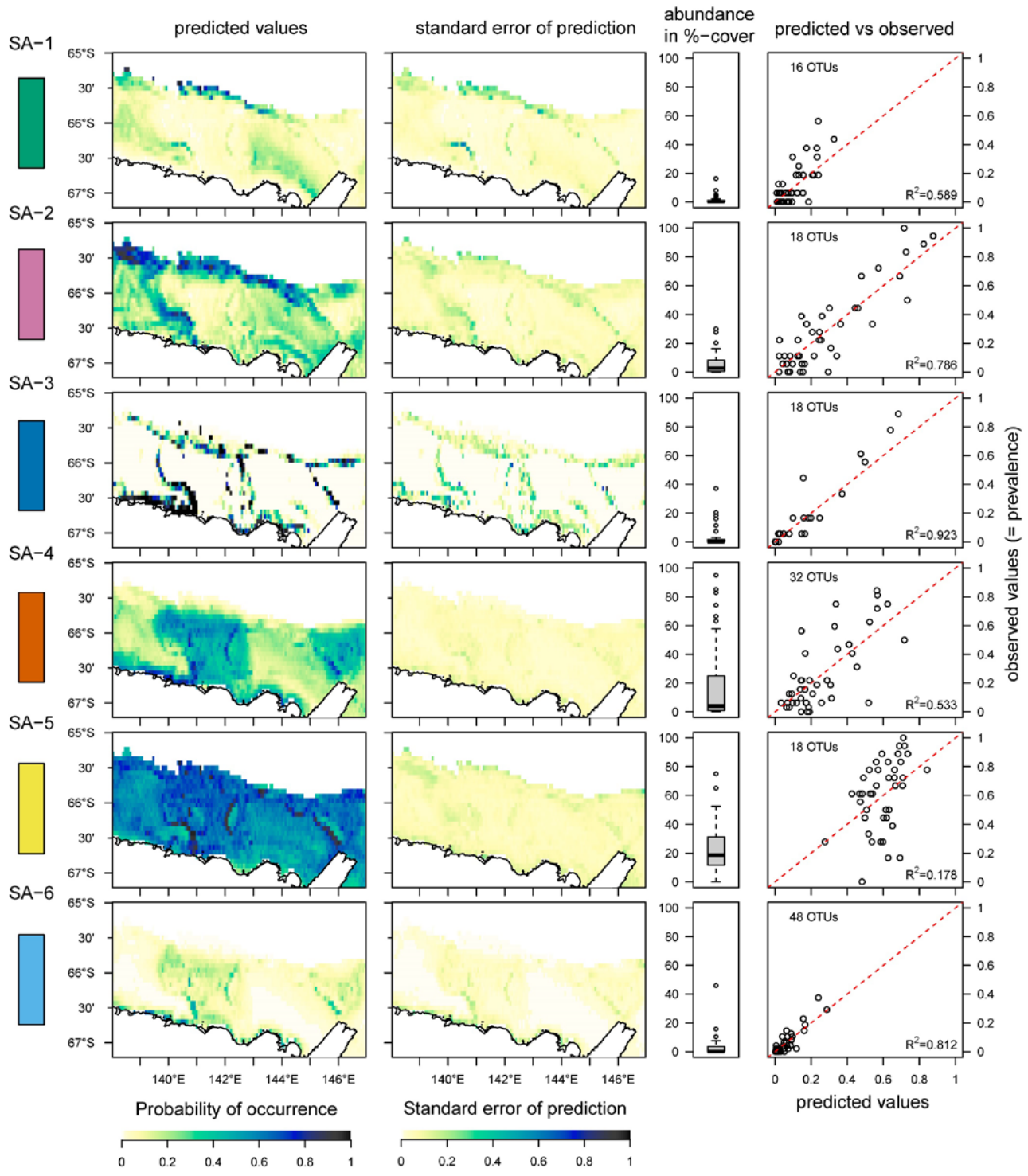


Figure 4.2: Distribution of six species archetypes **(SA 1-6)** identified from the OTU-dataset using the species archetype analysis, the standard error of the prediction, the total abundance of all OTUs combined within each SA and the relationship between predicted and observed values. A colour-code is added on the left side of the graphs for helping to compare this figure with figures 4.3 & 4.4. The red dotted line indicates the 1:1 line between predicted and observed values; the R2-value is for a linear regression between observed and predicted values. The predictions are based on data from 41 sites, and the area under the Mertz Glacier Tongue is excluded from the predictions.

4.3 Results

Classifying benthic fauna to the highest taxonomic resolution possible, we identified a total of 172 operational taxonomic units (OTUs) from 11 different phyla (Appendix C Table 1), belonging to 27 taxonomic and 30 functional groups. Many OTUs were rare, with 26 OTUs observed only once at the 41 sites, and half of all OTUs found at five sites or less. Only 17 OTUs were found at more than 20 sites, and six of these common OTUs represent unidentified taxa where individuals could not be distinguished further than to broad categories of Bryozoans, Sponges, Seastars, Ophiuroids, Holothurians and Actinaria. The most dominant phyla were echinoderms (38 OTUs), sponges (35 OTUs) and cnidarians (34 OTUs). In total, we found 54 mobile OTUs compared to 118 sessile OTUs. Most sponges (= active suspension feeders) were of a simple erect form or had a stalked base lifting them off the ground (Appendix C Tables 2 & 3). In contrast, most passive suspension feeders were branching in three dimensions.

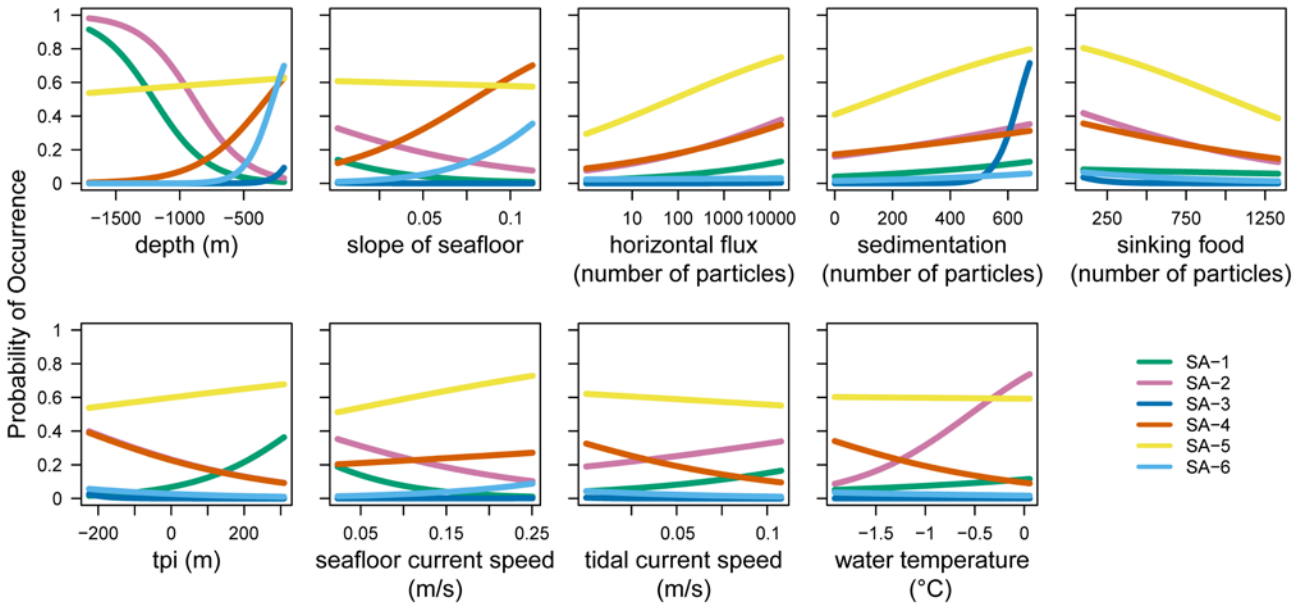


Figure 4.3: Probability of occurrence for the six species archetypes in relation to each of the environmental variables used in the analysis. A steep slope of a line means that the archetype changes strongly along this environmental gradient, indicating which environmental predictor variables are important in determining the presence or absence of species archetypes. tpi= topographic position index

4.3.1 OTU-level archetypes

The statistical analysis using species archetype models identified six distinct species archetypes (SAs, Fig. 4.2 & Appendix C Fig. 1) from the full dataset which contains benthic fauna classified to the highest possible taxonomic resolution (operational taxonomic units, or OTUs). All Species Archetypes (SAs) contain OTUs with a mix of functional traits and belonging to different taxonomic groups (Appendix C Tables 2-5). Predictions for OTU occurrences from the SAs match well with the observed values (R^2 between 0.533-0.923), with the exception of SA-5 (R^2 = 0.178). The strongest (steepest)

overall response from SAs is in relation to depth of the seafloor (Fig. 4.3 & Appendix C Table 6), but all environmental variables used in the analysis influence SA-distributions.

OTUs in SA-1 are mostly mobile with a few sessile taxa of simple body-shape, living in the deeper part of the continental shelf, where unconsolidated sediments prevail (Fig. 4.2, Appendix C Table 4). This assemblage is predicted with high probability on the slope near the Adelie Bank and Sill, but just outside of areas sampled in our study, meaning we cannot confirm these high values with our observations (see sampling sites in Fig. 4.1 and predicted vs observed for SA-1 in Fig. 4.2). SA-2 is an assemblage representative of the slope areas, and is dominated by sessile taxa. Generally, SA-1 and SA-2 share a similar environmental response apart from SA-1 occurring with a higher probability on higher topographic positions and SA-2 occurring in warmer waters (Fig. 4.3).

SA-3 is an assemblage containing species with a diversity of body-shapes and similar to SA-2, is dominated by passive suspension feeders (Appendix C Table 2). This archetype inhabits the edges of the banks and also occurs along the continental slope, typically in steep slope regions. SA-2 and SA-3 contain many taxa that classify as vulnerable marine ecosystems, meaning they are vulnerable to some fishing practices and deserve special protection due to their importance for ecosystem functioning (www.fao.org/in-action/vulnerable-marine-ecosystems).

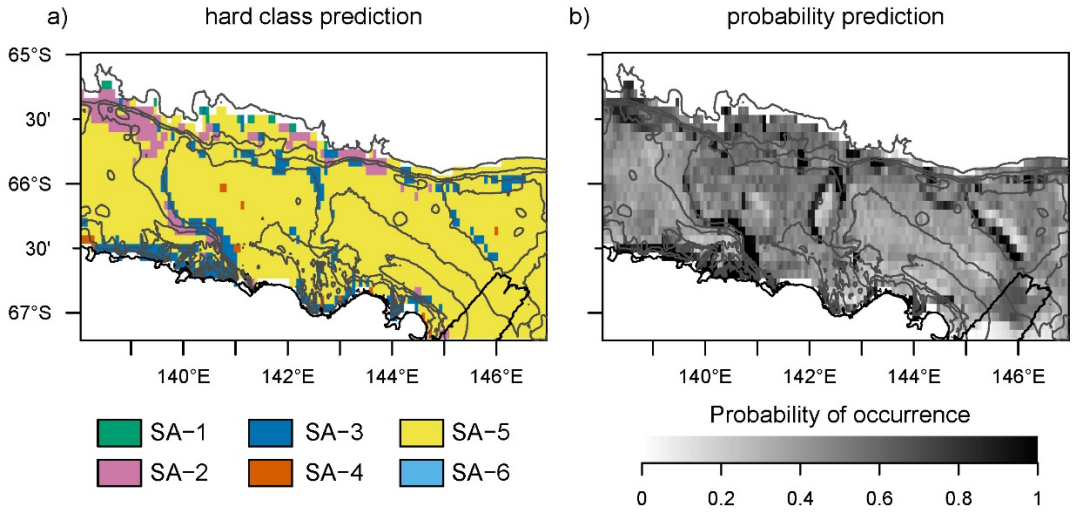


Figure 4.4: Hard classed distribution of six archetype predictions across the George V shelf, East Antarctica. Map **a**) identifies which group of species is most likely to be encountered at any specific prediction point across the study area. **b**) shows the probability of occurrence for the most likely archetype. These maps do not provide any indication of similarity or difference between sites for which a different analysis, such as regions of common profile (Foster et al. 2013), is needed. SA-6 never dominates the assemblage.

SA-4 contains common taxa, similarly to SA-5, but is restricted to the banks. This is a typical Antarctic assemblage with many suspension feeders and a diverse range of body-shapes. SA-5 dominates the benthic assemblage on most of the George V shelf (Fig. 4.4), and represents a diverse range of a few (18) very abundant and common OTUs with a broad distribution (see also Appendix C Table 4). Although the standard error of the prediction is low (Fig. 4.2) across the study region, comparing predicted and observed values reveals poor predictive power of this group (Fig. 4.2, last column, R^2 = 0.18). Thus, the OTUs comprising this group are relatively abundant and ubiquitous independent of

environmental variation. The response curve of SA-5 to environmental variables is shallow (Fig. 4.3), indicating that even strong environmental differences only lead to weak changes in this group. SA-5 contains four OTUs that represent unidentified taxa where individuals could not be distinguished further than the broad categories of Bryozoans, Sponges, Seastars and Ophiuroids.

SA-6 represents an assemblage with low abundance, and limited to shallow and steep sections on the shelf close to the coast and in locations characterised by muddy substrate, dropstones and relatively protected from icebergs (Marc Eléaume, unpublished data). This group largely responds to depth and slope but not to other environmental variables examined, and contains a mix of mobile and sessile taxa with many different body shapes (Appendix C Table 4). SA-6 is the only archetype that never dominates the benthic community on the George V shelf (Fig. 4.4).

All six SAs contain mobile and sessile species, but not every SA contains all categories of feeding type and body-shape (Appendix C Table 2). For example, only suspension feeders and predators can be found in SA-2, but there are no deposit feeders or opportunists present. Similarly, not every SA contains every body-shape. Flat body-shapes are absent from SA-2, erect stalked forms are absent from SA-3, barrel and tube-like sponges are absent from SA-1, SA-3 and SA-5, 2D-structured suspension feeders are absent from SA-1 and SA-5, no Anemones are found in SA-5 while tubeworms are found only in SA-3, SA-4 and SA-5. Ball-shaped forms are absent in SA-1 & SA-6 and massive sponges only occur in SA-6 (although only 3 OTUs fall into this category).

4.3.2 Taxonomic- and functional-group archetypes

In contrast to the analysis of the OTU-dataset, which reveals six species archetypes, the aggregated datasets of taxonomic groups (TG) and functional groups (FG) reveal three species archetypes respectively (Fig. 4.5). Both TG and FG archetypes show similar distributions, but all species archetypes show weak predictive power for the probability of occurrence (R^2 from 0.17-0.37, Fig. 4.5, predicted *vs* observed). Another similarity between TG- and FG-analyses is that each results in one archetype with abundant and very common OTUs (TG SA-1, FG SA-1), a second archetype with also abundant OTUs but not as common (TG SA-2, FG SA-2), and a third archetype of rare OTUs (TG SA-2, FG SA-2). Interestingly, despite these similarities, the OTU composition varies considerably between the TG- and FG-archetypes (Appendix C Fig. 2).

4.4 Discussion

Our results show distinct assemblages of benthic macrofauna can be identified with much greater confidence when using data comprising presence/absence of operational taxonomic units (OTUs) than when data describe *a-priori* determined taxonomic or functional groups. Although we expected the expert-grouped taxa not to perform as well as when using the more highly resolved data, the magnitude of differences was surprising to us, especially in regard to grouping by functional traits. In theory, if the functional traits selected truly correspond to species with similar responses to environmental conditions, we should (1) expect predicted values from the analysis of functional groups to fit similarly well to observed values as predicted values from the OTU-analysis, and (2) expect OTUs in each species archetype to be from mostly the same functional groups. However, our results show this is not

the case, and *a-priori* grouping of OTUs by functional or taxonomic similarity merges OTUs that do not respond to environmental conditions in the same way.

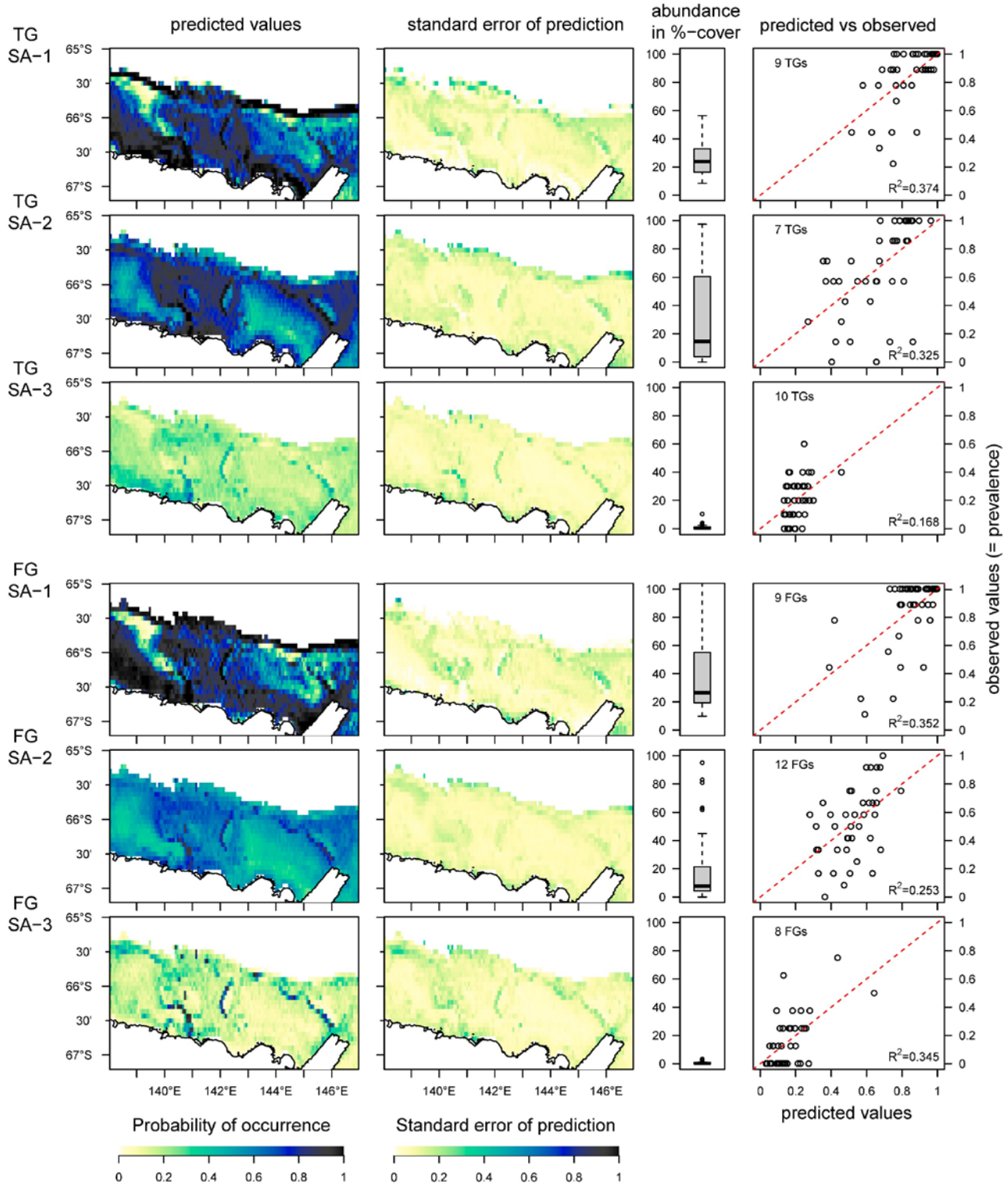


Figure 4.5: Predicted distribution of species archetypes identified from the taxonomic (TG) and functional group (FG) datasets, the standard error of the prediction, the total abundance of all OTUs combined within each SA and the relationship between predicted and observed values. The red dotted line indicates the 1:1 line between predicted and observed values; the R2-value is for a linear regression between observed and predicted values. The predictions are based on data from 41 sites, and the area under the Mertz Glacier Tongue is excluded from the predictions.

A possible explanation why the functional grouping poorly predicts the distribution of biodiversity is that the functional traits selected are not important in determining the presence or absence of these taxa, or are not important at all. Our results show most combinations of the three functional traits feeding-type, mobility and body-shape can be found in at least half of all species archetypes, in a wide range of environmental conditions across the study region, and are therefore not good surrogates for predicting the presence and absence of species. However, this result does not mean the functional traits selected are not important at all, because they could act on different levels of community structure, such as on the abundance of different species. Interestingly, a very broad grouping of taxa based solely on their feeding type, produces promising results for mapping patterns in the abundance of key components of the benthic community (Jansen et al. 2018a). More research is needed to resolve whether other functional traits not used here might be more suitable for predicting patterns in the presence and absence of species.

Another factor that influences the results is the taxonomic level at which to group species. In our study, we grouped species mostly at the class and phylum level. Classifying organisms into lower level taxonomic groups such as families is difficult when using image-data, because many family-specific features might not be distinguishable. Previous studies have also found that an aggregation at class or phylum level changes observed patterns in assemblage structure (Smale et al. 2010) and species distributions (Wodarska-Kowalczuk and Kedra 2007). However, although there are examples where family-level aggregations may be used as effective surrogates for diversity patterns (e.g. in molluscs: Terlizzi et al. 2009), any taxonomic rank higher than species can behave as a random group of species not providing ecologically meaningful information (Bevilacqua et al. 2012) and the outcomes of taxonomic groupings may vary between habitats and trophic levels (Sutcliffe et al. 2012). Our results suggest that presence-absence data should be classified to the highest taxonomic resolution where possible, and not amalgamated into either taxonomic of functional groupings when studying responses of Antarctic benthic communities to environmental conditions.

Our mapped predictions of the benthic communities on the George V shelf show similarities to previousl detailed descriptions and maps of the region (Post et al. 2010, Post et al. 2011, Jansen et al. 2018a). We can confirm that areas of particular interest (i.e. areas with rare assemblages, and a turnover of species archetypes) are shallow, steep habitats close to the coast or on the edges of the banks, and on the continental shelf break and slope. Vulnerable marine ecosystem (VME) taxa, which are of particular interest for management, have previously been detected and then protected from bottom fishing practices in two separate areas in this region (see Fig. 4.1). SA-2 and SA-3 are likely representative for the distribution of VMEs, and the mapped predictions can help finding further assemblages in need of protection. SA-4 and SA-5 are most similar to the distribution of seafloor suspension feeders mapped in an earlier effort in this region (Jansen et al. 2018a). Some small-scale features in SA-4 and SA-5, particularly on the Adélie bank, stand out, but should be treated with care, as they could be artefacts from the ocean model and the food-availability-maps that have translated into the predictive maps. More sampling in these interesting areas would help to clarify if such patterns exist. A proportion of the benthic community (i.e. SA-5) is difficult to predict, even with the cutting-edge statistical methods used here, which at least partially explains why the biogeography of Antarctic benthos has been found to be hardly predictable in other regions around the continent (Gutt et al. 2013c).

Nonetheless, the overwhelmingly high correlations between observed and predicted values from the species archetype models are encouraging, and we suggest model-based approaches should be a first choice when mapping Antarctic benthic communities.

Taxonomic resolution matters, and the level to which taxa in a dataset are identified influences the spatial patterns in biodiversity that are - and can be - observed. If resources such as time, money or expertise are limited, and taxa can only be identified at a broad taxonomic level, a more simplified and less accurate picture of the patterns of biodiversity has to be expected. Our study shows that – for the most part- the distribution of benthic fauna on the Antarctic continental shelf can be well explained by environmental conditions. This is a promising step towards mapping the distribution of Antarctic benthic fauna on a continental scale as a base for an informing management of this unique environment.

4.5 Acknowledgements

We would like to thank Rachel Downey for classifying the sponges, Tina Molodtsova for helping to classify the cnidarians, and the reviewers for their comments. Biological samples were collected during the CEAMARC program as part of the IPY #53 Census of Antarctic Marine Life program. Coastline and glacial features for the figures are taken from the Antarctic Digital Database version 5. JJ is supported by a Tasmanian Graduate Research Scholarship and a QAS Top-Up scholarship. This work was completed as part of Australian Antarctic Science project 4124.

Chapter 5

Combined assessment of the spatial distribution and structural dynamics of deep benthic Antarctic marine communities

This chapter has been accepted for publication (pending minor revisions) as an article under the same title in
Ecological Applications.

Jan Jansen[1,2], Piers K. Dunstan[3], Nicole A. Hill[1], Philippe Koubbi[4], Jessica Melbourne-Thomas[2,5], Romain Causse[4] & Craig R. Johnson[1]

[1] Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia
[2] Australian Antarctic Division, 203 Channel Highway, Kingston TAS 7050, Australia
[3] CSIRO Marine and Atmospheric Research, 3-4 Castray Esplanade, Battery Point TAS 7004, Australia
[4] Unité Biologie des Organismes et Ecosystèmes Aquatiques (BOREA), Muséum National d'Histoire Naturelle, Sorbonne Université, Université de Caen Normandie, Université des Antilles, CNRS,
[5] Antarctic Climate & Ecosystem Cooperative Research Centre (ACE CRC), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia
IRD, Paris, France

Abstract

Characterising the spatial distribution and variation of species communities and validating these characteristics with data from the field are key elements for an ecosystem-based approach to management. However, models of species distributions that yield community structure are usually not linked to models of community dynamics, constraining understanding and management of the system, particularly in data-poor regions. Here we use a dynamic network model to predict changes in Antarctic benthic community structure between major marine habitats characterised largely by seafloor depth and slope and use multivariate mixture models of species distributions to validate the community dynamics. Further, we then assess how future increases in primary production associated with anticipated loss of sea-ice will likely affect the ecosystem. Our study shows how the spatial and structural features of ecosystems in data-poor regions can be analysed and possible futures assessed, with direct relevance for ecosystem-based management.

5.1 Introduction

Ecosystem-based management, which aims to conserve ecological services while simultaneously meeting socioeconomic, political and cultural needs, is of key importance for sustainably managing natural resources now and into the future (FAO 2018). Fundamental to any ecosystem-based management is a thorough understanding of the functioning of the ecosystem of interest and the spatial distribution of its major components. The two main pathways to gather this knowledge from collected data are models of community dynamics which focus on the ecological structure and functioning of the system, and regionalisations which spatially categorise assemblages of species, functional groups, or other operational taxonomic units.

Ecosystem models allow testing hypotheses regarding the dynamics of interaction networks and the potential impacts of external drivers on ecosystem components. They have been fundamental for the management and assessment of extractive industries (e.g. Dambacher et al. 2015, Marzloff et al. 2015, Harvey et al. 2016), in cumulative impact assessments (e.g. Melbourne-Thomas et al. 2011a, Melbourne-Thomas et al. 2011b, Anthony et al. 2013, Gurney et al. 2013), in evaluating food-webs (e.g. Gillies et al. 2013, Melbourne-Thomas et al. 2013, Heymans et al. 2016), and in predicting changes in ecosystem attributes under scenarios for human use and environmental change (e.g. Fulton 2010, Melbourne-Thomas et al. 2011a, Melbourne-Thomas et al. 2011b, Blanchard et al. 2017). These kinds of fully quantitative models usually require detailed information about the rate of physical and biological processes in the ecosystem. In contrast, ecological regionalisations of ecosystems, which typically underpin spatial planning including assessments for Marine Protected Areas (e.g. Barrett et al. 2001, Jordan et al. 2005, Hill et al. 2017), focus more on high-resolution estimates of the spatial distribution of distinct assemblages of species, but cannot, for example, account for non-linear changes in interactions between species. A combination of both approaches allows complementary insight into ecosystems providing there is adequate validation by field-data.

However, as the physical environment changes in space, in both two- and three-dimensions, or through time, so do the interactions between the physical and the biological environment, influencing species

distributions and ecosystem functioning (Edwards and Richardson 2004, Hoegh-Guldberg and Bruno 2010b). This presents a challenge, particularly in data-limited regions where little is known about how biological communities change in space and through time, limiting the ability to both conserve the environment and ensure its sustainable use. Combining spatial and dynamic quantitative approaches could draw on the strengths of both models, while avoiding trade-offs that would be apparent if only one type of model were used (Levins 1966, 1993).

An environment that is comparatively little studied and not well understood is the deep ocean floor (here considered as anything below 200 m), one of the largest biomes on Earth. To date, deep benthic and demersal ecosystems have usually been broadly categorised into shelf, slope and abyssal habitats (e.g. O'Hara et al. 2011, Douglass et al. 2014, Woolley et al. 2016), with latitudinal gradients overlying species distributions (e.g. O'Hara et al. 2011, Woolley et al. 2013). However, the physical and ecological processes leading to the separation between these habitats and communities are not fully understood, and while species differ between the tropics, temperate and polar regions, ecological theory suggest fundamental processes influencing their distribution should be similar (e.g. Woolley et al. 2016). Although bathymetry may not directly influence most species, the 3D-structure, rugosity, slope, and other features of the sea-floor that are related to bathymetry serve as a proxy for important variables that influence many species, in particular determining whether the benthos at a particular location is characterised by hard or soft substrata, the local ocean current regime, food-availability, and sedimentation patterns. Therefore, it is important to consider bathymetric features to understand how the structure and functioning of benthic ecosystems differ in space (e.g. Hogg et al. 2016, Jansen et al. 2018b).

Recently, several new techniques have been developed that can make much greater use of sparse biological data (Dunstan et al. 2011, Melbourne-Thomas et al. 2012, Foster et al. 2013, Ovaskainen et al. 2017). New statistical techniques, such as Species Archetype Models (Dunstan et al. 2011), can group multiple species with similar responses to environmental factors together, enabling study of the distributional patterns of a much bigger proportion of the fauna than previously. Mapping these assemblages also reveals insights into spatial differences in community structure, an important factor for the functioning of an ecosystem. Another important recent development allows for statistical analysis of qualitative network topologies (Raymond et al. 2011, Melbourne-Thomas et al. 2012). Qualitative network topologies provide useful insights into ecosystems where data are too limited to fully parameterise an ecosystem model (Dambacher et al. 2009). The new approach uses press-perturbations of the system, combined with thousands of quantitative runs using randomly assigned magnitudes for every interaction while preserving the sign of the interaction, to reveal insight into how different nodes of the network respond to the simulated perturbation (Melbourne-Thomas et al. 2012). This enables a powerful test of the effects of putative ecosystem drivers on ecosystem functioning for little known systems.

In our study, we analyse both the spatial distribution and the network structure of the Antarctic benthic and demersal ecosystem using data from the East Antarctic continental shelf and upper slope (Fig. 5.1). We map the spatial distribution of demersal fish assemblages from trawl-data (Causse et al. 2011), compare the distributional patterns to mapped predictions of benthic macro-invertebrates from a previous study (Jansen et al. 2018b), and use these to quantitatively identify four distinct habitats characterised by depth and slope. We conceptualise the network topology of the broad Antarctic

benthic ecosystem, test how changes in depth and slope affect ecological structure and validate results from a dynamic network model with the mapped distributions of fish and macro-invertebrates. We also test how increases in primary production, a likely future scenario (Laufkötter et al. 2015), may affect the system. The analysis gives insight into the functioning of a biodiverse ecosystem in a remote environment and shows how predicted dynamics in community structure can be validated and located spatially using species distributions.

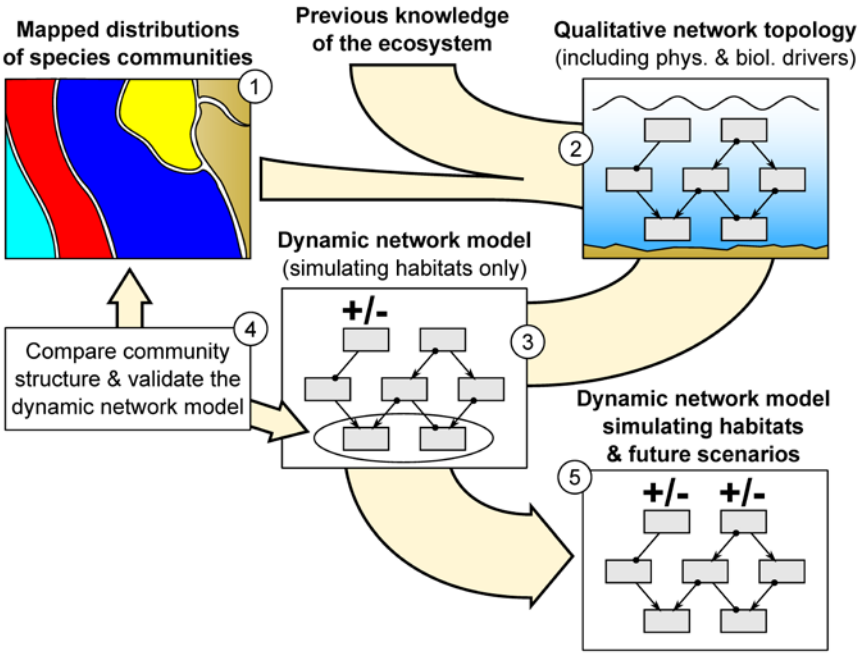


Figure 5.1: Overview of our approach combining spatial and dynamic models to learn about species community structure in different habitats and predict effects of a changing environment. **(1)** Mapped distributions of distinct communities are based on statistical relationships between 'species' (or operational taxonomic unit) distributions and environmental variables. In our study, we use species archetype models to map communities. **(2)** The qualitative network topology describes interactions between the species community and its physical (phys.) and biological (biol.) drivers. **(3)** Using press-perturbations of important physical drivers, the dynamic network model simulates the composition of species communities in different habitats. **(4)** Comparing predictions from the dynamic and the spatial model allows validating the network topology to ensure all key drivers are captured in the model, and that model responses to drivers are consistent with observations. Importantly, the combination of the two different models allows spatial definition of the boundaries of simulated habitats from the dynamic network model, and identification of species associated with each habitat. **(5)** Future scenarios, such as increased primary production near the Antarctic continent, can be simulated by press-perturbing biological drivers. Critically, these simulations give new insight into how the composition of species communities can respond to environmental changes.

5.2 Methods

5.2.1 Study area

The study region is the George V continental shelf and slope in East Antarctica, spanning latitudes 139°E to 147°E from the Antarctic coastline to the shelf break at around 65.5°S. The continental shelf in this region is typically between 500-700 m but punctuated by bathymetric features including the

Mertz and Adélie Banks (200-250 m depth) and the George V and Adélie Basins (depths up to 1300 m) (Fig. 5.2). The oceanography in this area is mainly influenced by the Mertz Glacier Tongue and the adjacent Mertz Polynya (Cougnon et al. 2013), an area of ice free water that drives water circulation (Massom et al. 2001) and supports a relatively long growing season of phytoplankton (Sambrotto et al. 2003, Beans et al. 2008). Demersal fish have been found to primarily inhabit the deeper inner-shelf depressions and their upper sides, and descriptive analyses of the region have found differences in the assemblage structure between the continental slopes, the basins and on the shelf (Koubbi et al. 2010, Causse et al. 2011). Diverse and abundant benthic macrofaunal communities are found along the shelf-break and on the shallower section of the shelf between 200-600 m (Post et al. 2011). Modelling work indicates widespread suspension feeder cover on the banks (Jansen et al. 2018a), and distinct assemblages of benthic macro-invertebrates particularly along the steep edges of the banks and the coastal and continental slopes (Jansen et al. 2018b). A more detailed descriptive analyses of the fish assemblages inhabiting the George V shelf can be found in Causse et al. (2011), and a detailed description of the benthic invertebrate communities in Post et al. (2011).

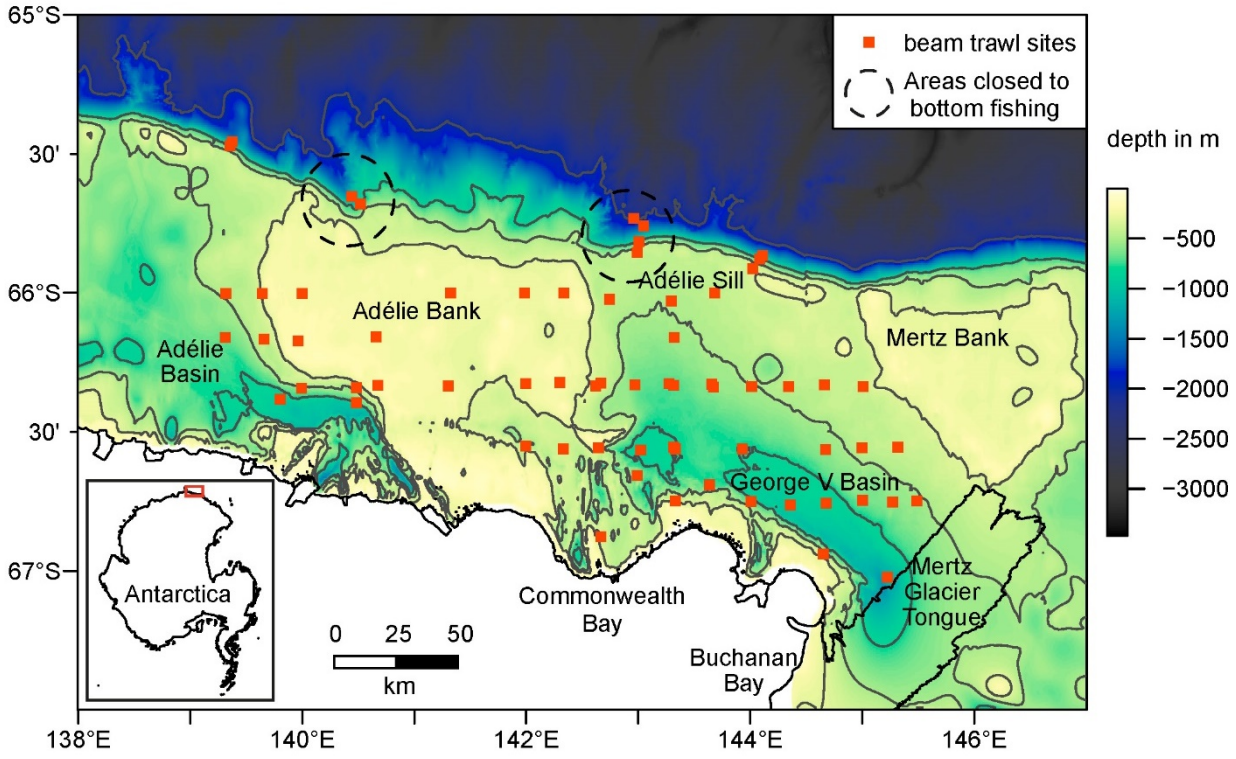


Figure 5.2: East Antarctic continental shelf in the George V region with trawl-sample locations. Background colours and contour lines in grey indicate depth (Beaman et al. 2011). All areas shallower than 550 m are closed to bottom fishing, as are the two deep areas (dotted circles) due to the presence of vulnerable marine ecosystems (Jones 2017). The inset map (bottom left) shows the location of the study area (red box).

5.2.2 Biological data

We used previously published data for abundances of demersal fish (Causse et al. 2011) and benthic macro-invertebrates (Robineau et al. 2018) from the George V shelf. All biological data were collected during the Collaborative East Antarctic Marine Census (CEAMARC) for the Census of Antarctic Marine Life from December 2007 to February 2008 (Hosie et al. 2011).

5.2.2-a Demersal fish sampling and identification

Beam trawls (3 m wide, 1.39 m high, mesh size in the cod end 10 x10 mm) were used to collect demersal fish at 66 sites. Trawls were placed along different environmental gradients covering banks, shelf depressions, coastal and continental slopes (Fig. 5.2), and covering the entire shelf from 139°E to 145°E. Trawl distance at the bottom was mostly between 500-1000 m (ranging between 85-1698 m) at depths of 150-2065 m. There was no spatial-, depth- or slope-related bias in the duration/distance of the trawls, and we accounted for the distance trawled in the analysis of the fish-abundance. There was a weak correlation between the distance trawled and the logarithm of the number of fish species found ($F_{1,64} = 5.861$, $P = 0.0183$). However, deriving a constant offset for a logit link function and a Bernoulli response is not possible, and therefore trawl distance was not included as an offset in the species archetype models. While univariate models may underpredict rare species, species archetype models are typically better at predicting rare species (Hui et al. 2013) giving confidence in the model outputs. Mounted video cameras were used to study avoidance of the trawl by fish.

Fish species were identified using Gon and Heemstra (1990), based on fresh or preserved specimens and, where possible, DNA barcoding. A total of 53 species belonging to 8 families were identified (Appendix D Table 1), with Nototheniidae the most abundant family (44.7% of individuals), followed by Bathydraconidae (19.8%) (Causse et al. 2011). A detailed description of sampling and identification, and a thorough descriptive analysis of the demersal fish diversity in the region can be found in Causse et al. (2011).

5.2.2-b Benthic invertebrate sampling and identification

Benthic invertebrate abundances were estimated from underwater still images, collected using a forward facing 8-megapixel Canon EOS 20D SLR with two speedlight strobes mounted on the beam trawls used to collect demersal fish. Hereafter, ‘trawls’ refers to the fish trawls and ‘transects’ refers to all still image transects. Still-cameras taking pictures every 10 seconds were deployed at 32 sites, and transect length was mostly between 4-6 km long, with the exceptions ranging between 3-16 km. Tow speed was 2.5 knots, and the average field of view of the seabed was 3.5 m, ranging between 0.6 to 7 m at times. A total of 2724 out of 3442 images were usable for analysis. The bottom third of each image was scored. For each image, the abundance of each species/morphotype was estimated within 5 % bins from 0 % to 50 %, and within 10 % bins from 50 % to 100 %.

Benthic invertebrates were identified to the highest taxonomic resolution possible. Where species identification was not possible, specimens with similar overall appearance were grouped into morphotypes (operational taxonomic units). A total of 172 benthic invertebrate morphotypes were identified and grouped into three feeding mode classes for analyses. A detailed list of identified benthic invertebrate morphotypes containing information about their taxonomic class, their feeding type and their association with the different species archetypes can be found in Appendix C Tables 1-4.

5.2.2-c Feeding modes of fish and invertebrates

Feeding mode is a functional trait that can play an important role in determining species distributions (e.g. Gaston 1987, Lombarte et al. 2003, Jansen et al. 2018c). In our study, we build a qualitative network topology based on the primary feeding modes of demersal fish and benthic macro-invertebrates and

validate the dynamic network analysis using quantitative information about species distributions (see section 'Dynamic network model (DNM)').

For each species of fish, we identified their primary feeding mode (either zooplankton, zoobenthos or nekton) using fishbase.com and published literature (see Lombarte et al. 2003, Duhamel et al. 2010) (Appendix D Table 1). We were unable to assign primary feeding modes to only seven species and excluded those species from validating the dynamic network model.

Benthic invertebrates from the region have previously been classified into suspension feeders, deposit feeders and predators by Jansen et al. (2018c), using their taxonomy and appearance along with expert knowledge. We used the previously published dataset containing the full list of species, their feeding types and abundances (Robineau et al. 2018).

5.2.3 Environmental data

For mapping the spatial distribution of demersal fish, we used the same environmental covariates considered for mapping the distribution of benthic invertebrates as in Jansen et al. (2018b). Specifically, we considered depth, slope of the seafloor and topographic position index derived from Beaman et al. (2011), ocean current speed, tidal current speed, and temperature at the seafloor derived from a regional oceanographic model (Cougnon et al. 2013), and three estimates for the availability of food at the seafloor from Jansen et al. (2018c) (i.e. food-particles arriving near the seafloor after sinking from the surface, horizontal flux of food along the seafloor, and food-particles settling onto the seafloor). We excluded environmental covariates that were highly correlated with variables already selected, such as surface productivity (highly correlated with the number of sinking particles arriving near the seafloor; Pearson's r = 0.971), and roughness of the seafloor (highly correlated with slope; Pearson's r = 0.992).

Similarly to Jansen et al. (2018b), we corrected exceptionally high values from the map of settling particles to a value of 1000 (35 out of 2515 grid-cells contained values between 1035-5122), as these high values are likely an artefact of the modelling process rather than a real pattern to be observed.

5.2.4 Statistical analysis

We used a multi-model approach for analysing the benthic ecosystem on the George V shelf (Fig. 5.1). We first mapped the spatial distribution of demersal fish in the region using Species Archetype Models (SAMs) and set up a network topology using previously published detailed descriptions of the Antarctic ecosystem (see section 5.2.4-b for details). We then ran a dynamic network model (DNM) using press-perturbations to simulate different habitats and compare responses of the species communities to the predicted species community patterns from the SAMs. Finally, we used the DNM to test how anticipated future increases in primary production will likely affect the species communities.

5.2.4-a Species Archetype Models (SAMs)

For statistical analysis of the fish-data, we used SAMs (Dunstan et al. 2011, Dunstan et al. 2013), which are based on generalised linear models, and group taxa with similar responses to environmental covariates into 'species archetypes' for modelling. We initially developed SAMs for both count-data (number of individuals per species) and presence-absence data, but a preliminary analysis using the count-data did

not show reliable results due to the high number of rare species, and the general low count of fish, which results in dataset-characteristics more similar to presence-absence data. Therefore, we converted our dataset to presence-absence data for analysis and used a Bernoulli distribution in the SAM-analyses.

For the SAM-analysis, we considered all the environmental covariates outlined in the section 5.2.3 'Environmental data' and additionally included the logarithm for slope and a quadratic term for depth to account for exponential and hump-shaped responses in the data. As suggested in Dunstan et al. (2011), we used Bayesian information criteria (BIC) for selecting the optimal number of species archetypes. We ran 50-iterations of the same model with random starts and extracted the BIC in each of these models to ensure that inference was based on the global maximum of the likelihood-surface. We then used the model with the optimal number of species archetypes, and the suite of maps of environmental covariates to predict the probability of occurrence of each species archetype across the study area. We restricted the prediction area to the continental shelf down to ~2200 m, the maximum depth that the beam trawl was deployed, and do not predict below the Mertz Glacier Tongue where we have no samples and where environmental conditions might differ to the study region.

For the statistical analysis, we used R version 3.3.1(R Core Team 2016), and SAMs were developed using the R-package 'SpeciesMix' (Dunstan et al. 2011).

5.2.4-b Dynamic network model (DNM)

Model setup

For describing and analysing interactions in the Antarctic benthic ecosystem, we used a DNM based on a qualitative network topology with signed digraphs (Fig. 5.3). We used previous detailed descriptions of this region and of the Antarctic benthic marine ecosystem (e.g. Beaman and Harris 2005, Gutt 2007, Koubbi et al. 2010, Post et al. 2010, Causse et al. 2011, Gutt et al. 2011, Post et al. 2011, Gillies et al. 2013, Post et al. 2017, Jansen et al. 2018c) to choose which components to represent in the network model, and the nature of their relationships. A detailed description for each node can be found in Appendix D Table 2.

For our analysis, we focussed on physical and biological interactions that are affected by changes in either depth, slope or food-availability. In our network topology, we use the simplified term 'pelagic food sources' to represent the complex pelagic ecosystem dynamics between primary production, zooplankton communities and the export of particulate organic carbon. While the strength of individual nodes in the pelagic ecosystem differs, general increases in surface primary production positively influence both the zooplankton abundance and the export of particulate organic carbon. This simplified representation reduces model complexity while still allowing to assess how overall changes in primary production affect the benthic ecosystem. We have chosen not to include icebergs in our network topology, which can play an important role in the ecosystem (Gutt et al. 2007) but are difficult to predict because of their stochastic occurrence. We also did not include non-tidal ocean currents because in contrast to tidal-currents, they are affected by depth and slope in a less consistent manner.

The nodes and interactions of the network model were then analysed using QPress (Melbourne-Thomas et al. 2012). QPress uses a simulation approach for evaluating uncertainty. We ran 10,000 simulations

of the network, where in each simulation a random value between 0 and 1 (or 0 and -1 for negative interactions) was allocated to each interaction in the network.

For simulating the four main benthic habitats determined from the SAMs, we simultaneously changed slope and depth by individually assigning either a positive or a negative sign (Appendix D Table 3). Further, to simulate anticipated future conditions of increased primary production (Jones et al. 2014) we increased pelagic food sources in each of those four habitat-simulations, resulting in a total of eight scenarios.

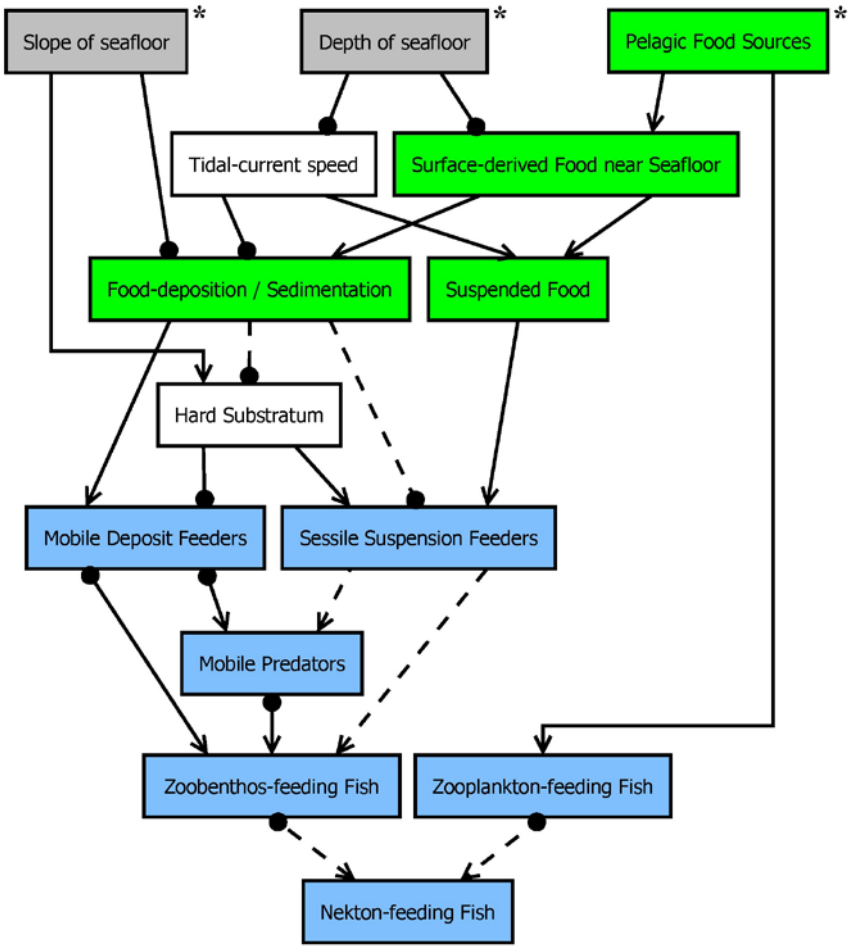


Figure 5.3: Qualitative network topology describing interactions and responses in the Antarctic benthic ecosystem. The colour code distinguishes between different categories of physical drivers (grey, white), ecological drivers (green), and key functional groups (blue). 'Pelagic food sources' included surface primary production, secondary production through zooplankton, and the export of this production towards the seafloor. An arrow-head shows positive influence; a circle-head shows negative influence; dotted lines indicate weak or uncertain interactions. The model also includes self-limitation for each component of the network (not shown on diagram). Drivers that we press-perturbed in the dynamic network analysis are marked (*).

Model evaluation

We evaluated the DNM-results for different habitats using the abundances of demersal fish from the benthic trawls (Causse et al. 2011), and the estimated cover of benthic invertebrates from Robineau et al. (2018).

For each species of fish/invertebrate, we calculated their mean abundance across all sites where they are present. We then aggregated the mean abundances for all species belonging to both the same Species Archetype and the same feeding-mode (Appendix D Table 4), which we used for comparison to the DNM-results.

For illustrating the spatial match between Species Archetype distributions based on presence/absences and the observed species abundances from the sample sites, we aggregated the abundances of all fish/invertebrates that occur in both the same Species Archetype and have the same feeding-mode for each site (Appendix D Fig. 1 & 2).

We adjusted fish-counts for sampling effort, by dividing through the distance trawled at each site. Estimates of the percentage cover of invertebrates did not need adjusting, because they are mean-values across transects.

For evaluating the spatial match between the distributions of species archetypes of benthic invertebrates and demersal fish, we've visually inspected the distribution maps and also calculated the correlation of values in the maps using the function 'rasterCorrelation' (Evans 2018) in R (Appendix D Table 5).

5.2.5 Data availability

The full dataset of demersal fish abundances is available through Causse et al. (2011). The benthic invertebrate data is available through Robineau et al. (2018).

5.3 Results

5.3.1 Species archetype models (SAMs) of demersal fish

Based on SAMs, we find five distinct assemblages of demersal fish on the George V shelf, each containing between five and 16 species from a total of eight families (Appendix D Table 1; a hard-classed prediction of the fish-assemblages summarizing their spatial distribution is given in Appendix D Fig. 5). Demersal fish can be found along three main habitat types, namely shallow banks (~200-300m), shelf depressions and the continental slope (Fig. 5.4). The confidence in the predictions is high (Fig. 5.4 & Appendix D Fig. 3).

Species Archetype A (SA-A) is made up of species belonging to the taxonomic families of Artedidraconidae, Bathydraconidae and Zoarcidae, and is predicted for deep (~400-1200m), flat habitat which has a lot of food arriving near the seafloor alongside a low topographic position index (i.e. which is typical for the inner-shelf depressions). Unexpectedly, the analysis suggests this assemblage is more likely to occur at low levels of sedimentation, which is atypical for the basins. The number of particles arriving near the seafloor and the number of particles settling on the seafloor are positively correlated in this area which potentially downplays the importance of settling particles in the model. Similar to SA-A, SA-B also occurs in the inner-shelf depressions but contains a wider range of taxonomic families with less common and less abundant species, and the model doesn't predict the occurrence of this archetype very well (Fig. 5.4 & Appendix D Fig. 3).

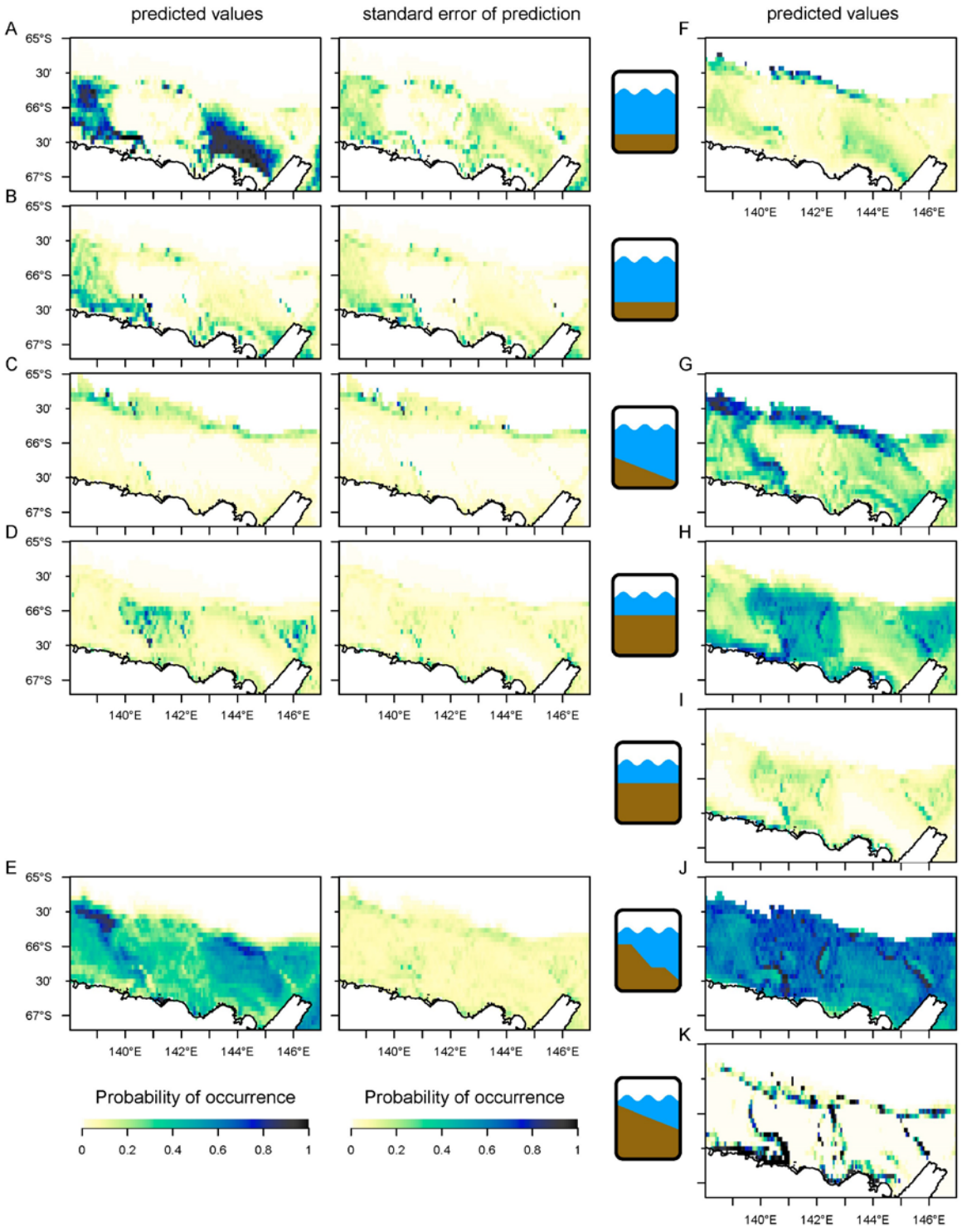


Figure 5.4: Comparison of species archetype model results for demersal fish species (**A-E**, this study), and for benthic invertebrates (**F-K**, from Jansen et al. (2018b)). The area under the Mertz Glacier Tongue is excluded from the predictions. Comic-icons in the column between fish and invertebrates indicate the main habitat corresponding to each pair of species archetypes. From top to bottom, these are: Deep-flat **(A, B & F)**, deep-steep **(C & G)**, shallow-flat **(D, H & I)**, widely distributed **(E & J)**, shallow-steep **(K)**. Species archetype models are based on observations from 68 sites (fish) and 41 sites (invertebrates).

SA-C is an assemblage dominant along the shelf-break and continental slope, preferring deep and steep habitat. It is comprised of equal amounts of zoobenthos- and zooplankton-feeding species, is dominated by species from Channichthyidae, Liparidae, Zoarcidae and contains the only Macrouridae and Muraenolepididae found in the samples. Although this species archetype is predicted mainly along the deep and steep shelf-break, zooplankton-feeding species also sometimes occur on the shelf (Appendix D Fig. 1).

SA-D contains a mix of feeding-types from a wide range of species and is predicted mainly on the shallower banks, where it occurs in low numbers. Certainty in the prediction is high, but the environmental preferences of SA-D are complex. Although the mapped predictions show higher probabilities on the shallower banks, the probability of occurrence for this archetype is higher for deeper and steeper habitat with a low topographic position index (Appendix D Fig. 4).

SA-E contains common, abundant and widely distributed species, mainly from the families Channichthyidae and Nototheniidae. The model shows a positive correlation between predicted and observed values, yet the relationship is relatively weak (R^2=0.364), and the model underestimated values where observed abundances are high (Appendix D Fig. 3).

The predicted spatial distribution of demersal fish shows similarities to the distribution of benthic macro-invertebrates in this region (Jansen et al. 2018b), which is highlighted in Fig. 5.4 (F-K) and in Appendix D Table 5. Assemblages most strongly correlate in the deep habitats (SA- & SA-C with SA-G, Pearson's r = 0.491 & 0.491) and on the shallower sections of the shelf (SA-D with SA-H & SA-I, Pearson's r = 0.353 & 0.436). Assemblages on the steeper sections of the shelf differ between demersal fish and benthic macro-invertebrates. The corresponding assemblage of benthic macro-invertebrates to SA-C (Fig. 5.4G), differs to the fish in that it is not only distributed along the shelf-break but also along the edges of the banks on the shelf.

5.3.2 Dynamic network model

The dynamic network model (DNM) aims to capture the main environmental and biological processes influencing seafloor communities in the region. Based on the mapped species distributions from the SAMs, we created a DNM (Fig. 5.3) and used press-perturbations to simulate how the key 'drivers' (depth and steepness) of community structure change across the four main habitats (i.e. deep-flat, deep-steep, shallow-flat, shallow-steep) (Fig. 5.5). To validate the simulated effects of the drivers on community structure in the DNM, we used the abundances of seafloor fauna in the species archetypes corresponding to each of the four habitats (see Methods section for details). After validating the DNM, we then tested how increasing pelagic food sources (primary production and zooplankton), a likely future scenario, might influence benthic ecosystem structure (Fig. 5.6).

The results from simulating different benthic habitats using press-perturbations on depth and slope as key 'drivers' largely agree with the changes in abundances of major fish and invertebrate categories observed from the SAMs (19 out of 27 cases, Fig. 5.5). In half of the eight cases where predictions from the DNM and observations disagree, the differences are very small and arguably not ecologically relevant (Fig. 5.5 & Appendix D Fig. 6). The overall high agreement with predictions suggests that the DNM adequately represents this ecosystem.

The comparison of habitats shows that when moving from a shallow to a deeper habitat, relative abundances of deposit feeders and zooplankton-feeding fish increase, while all other groups decrease. When moving from a flat to a steep habitat, abundances of suspension feeders and zooplankton-feeding fish increase, while all other groups decrease.

	P	O	P	O	P	O	Functional groups
shallow-flat 	-	-	-	-	+	-	Suspension feeders
	+	+	-	-	-	-	Deposit feeders
	-	-	-	-	-	-	Predators
	+	+	+	+	+		Zooplankton-feeding fish
	-	+	-	+	-		Zoobenthos-feeding fish
	-	-	-	-	-		Nekton-feeding fish
deep-flat 			+	+	+	+	Suspension feeders
			-	-	-	-	Deposit feeders
			(-)	(+)	(-)	(+)	Predators
			+	-	-		Zooplankton-feeding fish
			-	-	-		Zoobenthos-feeding fish
			(-)	(0)	0		Nekton-feeding fish
deep-steep 					+	+	Suspension feeders
					(-)	(+)	Deposit feeders
					+	+	Predators
					-		Zooplankton-feeding fish
					+		Zoobenthos-feeding fish
					+		Nekton-feeding fish
shallow-steep 							

Figure 5.5: Cross-comparison of changes in macro-invertebrate and fish functional groups between Antarctic benthic habitats. Predicted change ('P') for each functional group is the trend change in total positive outcomes after 10,000 press-perturbations of the dynamic network model. Observed change ('O') is the change in functional group abundance approximated through the species archetype models (see methods for details on the calculation). Table is read from top-left to bottom-right, e.g. moving from a shallow-flat to a deep-flat habitat, the dynamic network model predicts a decrease in suspension feeders (-), which is confirmed by the observed values (-). Highlighted in red are instances in which observed values do not confirm the predicted changes. Highlighted in parentheses are instances in which observed values also do not confirm predicted changes, although in these cases the differences are only small and not ecologically meaningful (e.g. slight positive versus slight negative, see Appendix D Fig. 6 for absolute values). Note that the species archetype models suggest that there is no distinct assemblage of demersal fish which inhabits the shallow-steep environment, which is why there are no data for demersal fish in the last column

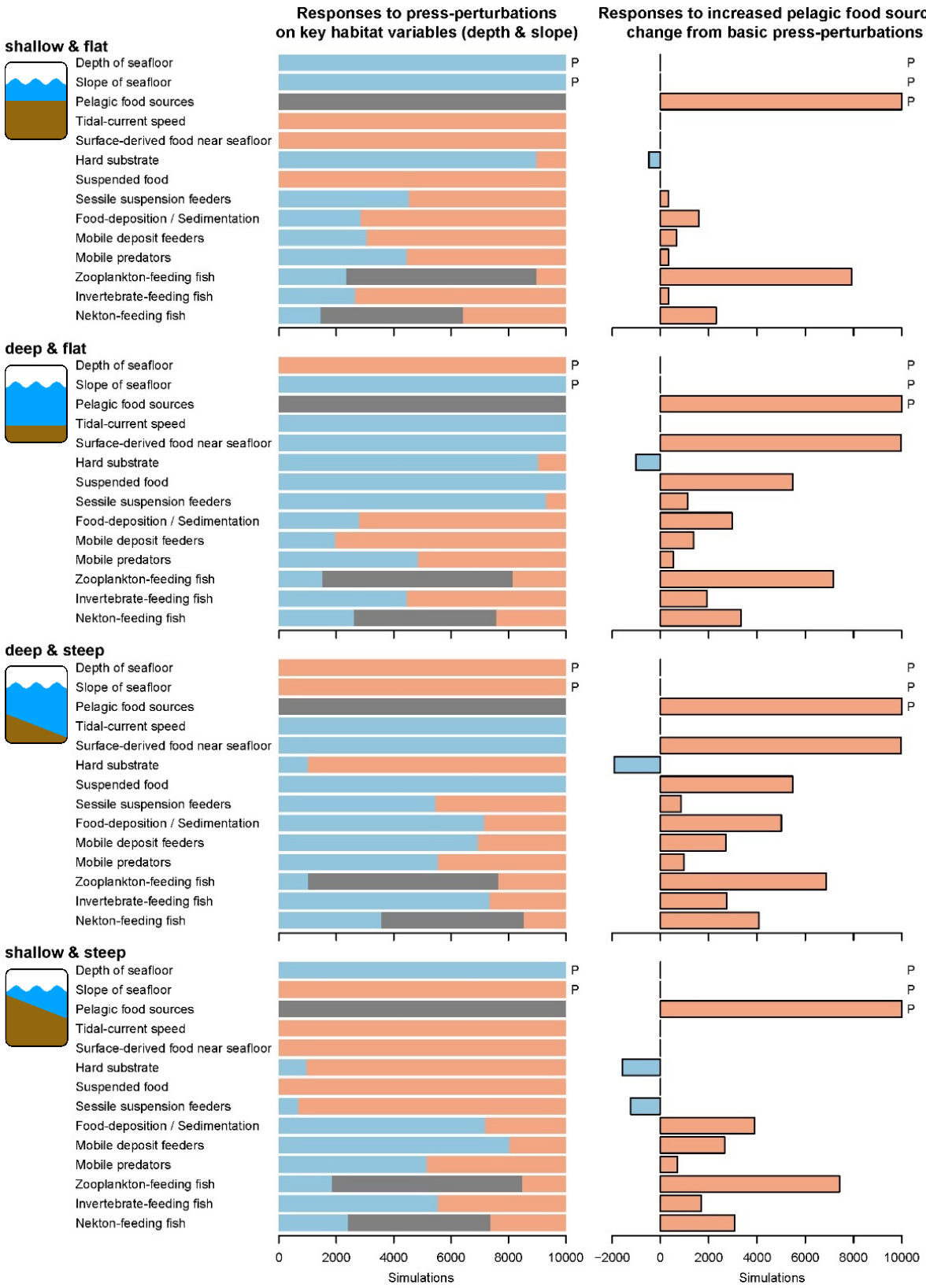


Figure 5.6: Evaluation of Antarctic benthic and demersal community responses to press-perturbations of the dynamic network model (10,000 simulations). To simulate the four main habitats, we used four combinations of negative/positive effects on depth and slope (Appendix D Table 3). Red indicates how often the component increases and blue how often it decreases as a response to the perturbation. Grey indicates how often responses are neutral because of weak or non-existing

links through the network. Variables that are press-perturbed in the analysis are marked with 'P'. The left-hand column (labelled 'Responses to press-perturbations on key habitat variables') shows how different components of the ecosystem respond to a change in the habitat (e.g. moving into a shallower and flatter habitat, the amount of surface-derived food near the seafloor increases). The right-hand column shows the difference between the basic model with change in only depth and slope, and when pelagic food sources increase in addition to a change in depth and slope.

The validation data shows that shallow-steep habitat contains less suspension feeders than shallow-flat habitat (Fig. 5.5, top row), which contradicts the predictions from the DNM. The other discrepancies in our results are that zooplankton-feeding fish are predicted to increase from deep-flat to deep-steep habitat while the observed data show a decrease, and that zoobenthos-feeding fish generally prefer deep habitat more than our DNM suggests.

Increasing primary production and thus zooplankton abundance and particulate organic carbon export, which is an expected future scenario on the Antarctic continental shelf (Jones et al. 2014), results in increased abundances of most seafloor fauna in the simulated habitats (Fig. 5.6). Hard substrata decrease in all habitats due to the increased sedimentation, and only shallow-steep suspension feeders decrease slightly. The model simulates surface-derived food near the seafloor already at saturating levels in shallow habitat prior to increasing primary production, and therefore increases in surface-derived food only increase the sedimentation-load with negative influence on suspension feeder abundances.

5.4 Discussion

Characterising the spatial and structural dynamics of ecological communities and validating these patterns with data from the field is key for an ecosystem-based approach to management. Validation of our dynamic network model (DNM) using species archetype models (SAMs) combines two very different approaches, and draws on the strengths of both models, avoiding trade-offs that would be apparent if only one type of model were used (Levins 1966, 1993). The DNMs allow both describing the ecosystem and network topology qualitatively and simulating system-level effects of future change, and the SAMs allow describing distinct community assemblages and locating where they occur. This is particularly relevant for areas with limited data, such as the Antarctic or parts of Africa and Asia, where ecosystem characterization will be crucial for developing an ecosystem-based management of marine resources (FAO 2016).

The DNM we present here, although simple, explains most qualitative changes in faunal abundance observed between the four main seafloor habitats. While our study focusses on East Antarctica, the general characterisation into bathymetric classes should hold true not only around the Antarctic continent, but also on other continental shelves and slopes around the world (see e.g. Danovaro et al. 2010, O'Hara et al. 2011, Woolley et al. 2016). The main difference from the Antarctic to lower latitudes will be related to temperature and seasonality, both of which influence the magnitude of interactions among functional groups in pelagic and benthic systems. For example, particles from phytoplankton blooms at higher latitudes are usually exported to the deeper ocean in higher proportions than at lower latitudes where particles decompose faster during sinking due to higher temperatures and different pelagic food-web dynamics (Lutz et al. 2007, Siegel et al. 2014). However, these differences should not fundamentally

change the structure of the system, i.e. deep-flat habitats should still receive more sedimentation than shallow-steep habitats, with concomitant effects on the distribution of fauna. Thus, similar network topologies to those used here can possibly be applied to other regions with limited data.

Although often described as pristine, Antarctic waters have already experienced measurable change (Walther et al. 2002, Constable et al. 2014, Gutt et al. 2015), and will undergo further change in the future due to climate change (Jones et al. 2014, Griffiths et al. 2017). The predicted decrease in sea-ice cover and an increase in melting will likely lead to higher primary production in certain areas, fuelling growth of fauna on the seabed (Barnes 2017) and increasing sedimentation. Our results suggest that increases in pelagic food sources are unlikely to lead to major structural changes in benthic communities, as almost all elements in the DNM increased in similar proportions. However, other factors that will change in the future, such as temperature and ocean acidification, are not captured in our network model, but are likely to affect the distributions of species and functional groups differentially (Constable et al. 2014, Griffiths et al. 2017, Marzloff et al. 2018). For example, increases in temperature to above 0°C could lead to shifts from species-communities tolerant to freezing temperatures to more generalist types of species communities (Griffiths et al. 2017). Because SAMs aggregate the distributions of single species, they can be used to validate additional functional aspects of assemblage structure that form part of a network model, depending on how much is known about the individual species. Incorporating these factors in a more comprehensive DNM can help to better understand whether and how different parts of the ecosystem are likely to change in the future. Further, a network model that incorporates different habitats, or includes estimates for how the ecosystem changes in the transition between habitats, can be used to test how changes in climate or other human pressures such as fishing affect those habitats, facilitating better management of ecosystem pressures.

Our combined assessment shows bathymetry and slope characterise the Antarctic benthic ecosystem into four main habitats, namely the various permutations of shallow/deep and flat/steep. In general, the large bathymetric features corresponding to these habitats are the shallow banks, the steep slopes along the banks and near the coast, the deep inner-shelf depression and the deep and steep continental shelf-break with the upper slope (Fig. 5.2). On top of this main bathymetric characterisation, pelagic food sources and other factors such as ocean currents or disturbance through icebergs (not considered here) affect the system. Indeed, in our case the location of the highly productive Mertz polynya over the deep-flat section of the shelf can explain some of the differences between predictions and observations, such as why we observe more zooplankton-feeders than predicted on the deep-flat than on the deep-steep section of the shelf. In contrast, the abundance of suspension feeders in the shallow flat habitat might be under-predicted because the bathymetry data does not capture small-scale steep features on the largely flat banks. Generally, our results are consistent with previous evidence that bathymetry and its derivatives influence the spatial distribution of species and communities in the Antarctic benthic and demersal ecosystem (e.g. Barry et al. 2003, Beaman and Harris 2005, Post et al. 2010, Douglass et al. 2014, Post et al. 2017, Jansen et al. 2018c). However, we show how bathymetry changes the dynamics of physical and biological processes that influence species communities, providing a better understanding of how different habitats might respond to future changes.

In conclusion, we have shown how our integrated approach can be used to analyse the spatial distribution and the structural dynamics of benthic communities in a diverse but data-limited region. Our integrated approach suggests that no major changes will occur in benthic community structure as result of increased primary production in the future, an insight we could not have gained from using just a single model. The four main habitats identified, described and simulated are commonly found in marine ecosystems globally, and the SAMs give us confidence in the topology of the qualitative network while also allowing insight into where specific habitats and functional groups can be found across the study area. We suggest that incorporating directly into DNMs how depth and slope influence ecosystem relevant mechanisms will allow to better investigate how species community dynamics change in space and through time, with particular relevance for data-limited regions such as the Antarctic.

5.5 Acknowledgements

We thank Guy Duhamel for helping to identify feeding strategies of demersal fish. Biological samples were collected during the CEAMARC program as part of the IPY #53 Census of Antarctic Marine Life program. Coastline and glacial features for the figures are taken from the Antarctic Digital Database version 5. JJ is supported by a Tasmanian Graduate Research Scholarship and a QAS Top-Up scholarship, and has received funding from the Institute of Marine and Antarctic Studies, University of Tasmania, to undertake essential research for this study at the Muséum National d'Histoire Naturelle in Paris, France. This work was completed as part of Australian Antarctic Science project 4124, the French Zone Atelier Antarctique of CNRS and the French ICOTA project 281 from IPEV.

Chapter 6

General discussion

This chapter has been prepared as a review article under the title ‘Predicting marine biodiversity’ for submission in *Science*.

Jan Jansen[1,2], Skipton N.C. Woolley[3], Piers K. Dunstan[3], Scott D. Foster[3], Nicole A. Hill[1] & Craig R. Johnson[1]

[1] Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, 20 Castray Esplanade, Battery Point TAS 7004, Australia

[2] Australian Antarctic Division, 203 Channel Highway, Kingston TAS 7050, Australia

[3] CSIRO, 3-4 Castray Esplanade, Battery Point TAS 7004, Australia

Abstract

Biodiversity is nature's most valuable resource, yet current rates of biodiversity loss are unprecedented in human history. While the challenge to better conserve biodiversity is well recognised in international treaties, the process of how to produce the knowledge required to best do so is not. Here, we review recent statistical developments for modelling biodiversity, methods for obtaining biological and environmental data, and approaches for linking biodiversity prediction with dynamic process models. Taken together, these improvements mark a step-change in biodiversity prediction from local to global scales. Although more technically challenging than other methods, statistical models allow more accurate predictions of how biodiversity is distributed, allow us to address the most relevant ecological questions, and allow to explicitly quantifying prediction-uncertainty. Combining key attributes from statistical and dynamical process models in an integrated approach can improve understanding of the space-time dynamics of ecosystem functioning and lead to greater confidence in management decisions for the mutual benefit of marine ecosystems and humanity.

6.1 Introduction

Biodiversity is nature's most valuable resource (Tilman et al. 2014) and profoundly influences humanity (Chapin Iii et al. 2000). It is a key element of ecosystem function and stability (Gamfeldt et al. 2015, Pennekamp et al. 2018), affects a wide range of important ecosystem services from food-production to disease-control (Cardinale et al. 2012), and its role is well recognised in a number of international conventions and treaties (e.g. Resolution 72/249 UN General Assembly, SCBD 2012, CCAMLR 2018). However, current human-induced biodiversity loss is estimated to be a thousand times faster than the background rate (De Vos et al. 2015). Reversing this unprecedented loss rate is one of the greatest and most important challenges of our time. Fundamental to tackling this challenge is to understand where and how biodiversity is distributed, and how these patterns are likely to change into the future, without which it is impossible to avoid further significant impacts from human activity.

Understanding where and how biodiversity is distributed can help with formulating (e.g. Reyers et al. 2007, Hauck et al. 2013), implementing (e.g. Hauck et al. 2013), monitoring (e.g. Jones 2011) and reviewing (e.g. Hill et al. 2017) the economic, social and environmental decisions that protect biodiversity from further decline (Guisan et al. 2013). However, because sampling comprehensive biological data is difficult and expensive, particularly in the oceans, there is a mismatch between what biological data are available and what we need to know to inform the important decisions that help protect biodiversity. Biodiversity predictions based on the relationship between relatively sparse biological samples and readily available comprehensive maps of environmental data are necessary to bridge this knowledge gap. While a key use of biodiversity predictions has been (and still is) to develop networks of protected areas (i.e. to meet Aichi Target 11 (SCBD 2012)), biodiversity prediction is also fundamental to any kind of spatial management that requires an understanding of the ecological structure and functioning of an area, such as risk assessment underpinning management decisions (e.g. Fordham et al. 2011, Keith 2015) and the management of fisheries (e.g. Foster et al. 2015, Anderson et al. 2016).

Despite that the importance of understanding how biodiversity is distributed in space and time is recognised widely, we have until now been limited in our capacity to deliver this information. Lacking biological and environmental data are key issues, but so are the technical challenges in analysis, including accounting for important data characteristics (Warton et al. 2015a). These problems can reduce our confidence in the reliability and interpretability of predictions, and restrict the kinds of ecological questions that can be investigated. However, recent developments in attaining and distributing biological and environmental data, in computational power, and in statistical methods suggest a step-change in capacity to predict biodiversity from local to global scales. Although more challenging than other methods, statistical models allow not only better validated and more precise predictions of how biodiversity is distributed, but they also allow estimating the uncertainty associated with predictions so that the results are more robust and more comprehensively interpretable than alternative approaches.

Here, we cover a range of topics that are key for predicting the distribution of biodiversity. Although the focus is on marine biodiversity, many of the developments outlined are relevant for any environment. First, we summarise different motivations that underpin the need for biodiversity predictions. Then we consider the limitations of biodiversity prediction given the kind of biological and environmental data available and outline some of the limitations and efficacies of commonly used methods. We introduce new developments that address these limitations and allow predicting biodiversity with unprecedented quality. Finally, we suggest how the recent developments in biodiversity prediction can be integrated with considerations of community and ecosystem dynamics to produce more informed and sophisticated predictions of biodiversity dynamics into the future.

6.2 What do we need to predict?

Ecological systems are complex, and there are many facets of biodiversity (Swingland 2001). In theory, we will only know everything about the biodiversity of an ecosystem once we know the characteristics and the distribution of every species it contains and understand the genetic flows within its populations. However, it is unrealistic to be spatially comprehensive in gathering this kind of knowledge for a natural system and so prediction is necessary to fill important knowledge gaps. What we need to predict can therefore vary widely depending on what aspect of the ecosystem we set out to understand.

The basic characterisation of a region to determine its biodiversity is often the aim of exploratory analysis of remote and/or difficult to access regions (usually this focusses on the abundance and richness of species that can be found, e.g. Dunstan et al. (2012)). Traditionally, sparse biological data may be used for descriptive analysis, or data may be reduced to biodiversity indicators such as richness to characterise general biodiversity patterns (e.g. Foster and Dunstan 2010, Dunstan and Foster 2011). In contrast, biodiversity predictions in better known ecosystems often have a specific aim that is relevant to their current use. Thus, what we need to predict can be the distribution of single species (or species groups) which are iconic and/or threatened (e.g. Pirotta et al. 2011, Brower et al. 2017), relevant for fisheries (e.g. Foster et al. 2015, Anderson et al. 2016, Champion et al. 2018) or useful surrogates for ecosystem health or ecosystem services (e.g. Young et al. 2015, Jansen et al. 2018a). If the aim is holistic spatial planning, such as for conservation planning and management, then predicting a single species' distribution is usually not sufficient, and a more comprehensive analysis of biodiversity is required. Multi-species

distributions can address similar questions to single-species distributions or biodiversity indicators, but additionally allow, for example, defining areas with similar species assemblages for spatial planning (e.g. Hill et al. 2017). This kind of more comprehensive knowledge is important for understanding how ecosystems function, how ecosystems might change in the future and how resilient they are to change, which underlies spatial planning important for management and conservation.

6.3 Limiting factors for biodiversity predictions

Any prediction of biodiversity is constrained by the nature and amount of biological and environmental data available, and by the methods used in analysis. In this section, we characterise how common limitations have to date hindered more comprehensive, accurate and reliable predictions of biodiversity.

6.3.1 Limitations in biological data

A major limiting factor for biodiversity prediction is what biological/ecological data are available for analysis, and how well the spatial and temporal scales at which the biological data are collected match the scales at which management is considered. Due to external restrictions (or incentives) such as funding, ease of access or weather patterns, biological data are often highly aggregated in space and/or time (e.g. Boakes et al. 2010, De Broyer et al. 2014, Isaac and Pocock 2015) and can contain a number of biases, which, if not carefully considered or accounted for in analysis, can dramatically influence the results of biodiversity predictions (e.g. Warton et al. 2013) and management outcomes (e.g. Grand et al. 2007). Potential issues with biological data can arise from how the data are collected, such as what type of gear or which individual has been used to collect/analyse the data (e.g. Harmelin-Vivien and Francour 1992, Warton et al. 2013), or in which environment these data have been collected, such as in food-rich or food-poor environments (e.g. Dayton and Oliver 1977). Further, the timing of the sampling is important, such as whether samples have been collected during day or night, during winter or summer, or during El-Niño or La-Niña years (e.g. Rooker and Dennis 1991, Holbrook et al. 1994, Godınez-Domınguez et al. 2000).

Apart from the way biological data are physically sampled, the way biological data are recorded and compiled inadvertently influences what type of biodiversity patterns can be predicted from them. Are species identities recorded or higher taxonomic levels, or are individuals identified by a common functional trait? Are only presences of species recorded, or are both presences and absences of species recorded? Are species' abundances recorded, and have they been recorded as the number of individuals, as biomass, or as percentage cover? For example, aggregating or identifying species at higher taxonomic levels such as order, class or phylum changes patterns in the diversity and distribution of arctic benthic macrofauna (Wodarska-Kowalczuk and Kedra 2007) and temperate macroalgae (Smale et al. 2010), but these changes may not be consistent and vary depending on the habitat and the trophic level considered (Sutcliffe et al. 2012). Similarly, grouping species according to major functional traits changes the predicted distributional patterns of Antarctic benthic macrofauna compared to an analysis of ungrouped data (Jansen et al. 2018b). The extent to which these types of groupings influence diversity patterns may additionally depend on whether abundance or presence-absence data are used because the *occurrence* of certain functional traits might be influenced in a different way by the environment than their *prevalence*. As an example, the availability of surface-derived food at the seafloor influences

the abundance but not the richness of benthic suspension feeders (Jansen et al. 2018c). The way biological data are recorded and compiled (either before or during analysis) can therefore influence the complexity and confidence in the spatial predictions and whether important spatial features of species distributions are detected (Jansen et al. 2018b).

Biological data can be particularly limited in large-scale analyses attempting to combine data from different studies. In these cases, the sampling method and the level of species identification may vary strongly between surveys and regions given different levels of taxonomic expertise and funding. Therefore, aggregating even high-quality biological datasets from different surveys and regions is difficult and potentially problematic, and, as a result, large-scale or global datasets (such as OBIS) usually contain only information about species occurrences and not their absences or abundances, limiting the biodiversity information that can be obtained from these data.

6.3.2 Limitations in environmental data

Sensible biodiversity predictions require using environmental factors in the predictions that are relevant to the species' distributions. However, biologically relevant environmental predictor variables are often missing from analyses, especially for fine-scale data sets. Instead, variables that correlate, but have no direct causal relationship with species (such as latitude), are used for prediction. While these kinds of variables can correlate with observed biodiversity patterns and help to understand coarse global trends in biodiversity pattern (e.g. Chaudhary et al. 2016), reliability in patterns based on these variables, their transferability to other regions and ecological interpretation can be limited (Gillman et al. 2015). Importantly, if biologically relevant environmental variables are missing, biodiversity patterns can be misattributed to other sources, or missed altogether – correlation is not causation. Further, missing variables that are important determinants of distributions can result in residual spatial autocorrelation in statistical analyses that violates the assumptions of many models, and can lead to overly confident predictions and estimates of the importance of environmental variables (Dormann et al. 2007, Guélat and Kéry 2018). This is particularly problematic if poor models are then used to support management decisions or to estimate future changes. Today, there are still a wide range of potentially important environmental variables not regularly available for biodiversity analyses. Major missing variables include the availability of surface-derived food at the seafloor (Jansen et al. 2018c) and, most notably, high resolution bathymetry and backscatter data (useful for determining substratum type) for the majority of the ocean (Mayer et al. 2018). These omissions limit our ability to model known regional biodiversity hotspots such as smaller reef systems, canyons, seamounts and other features in global analyses.

When important environmental variables are available for analysis, there can still be issues regarding their usage. Some environmental variables might include biases, noise or uncertainty that is not obvious to the user (such as limited detection of deep phytoplankton blooms using satellite remote sensing, see Blondeau-Patissier et al. (2014)), or the variables might not be useful because of their spatial or temporal resolution. The spatial and temporal resolution of environmental variables is important, particularly when they vary strongly on small scales (e.g. substratum, slope of the seafloor) or when analysing the distribution of highly mobile species. The coarser the resolution of a variable (both spatial and temporal), the more the variance is smoothed out, leading to a higher chance of

missing important spatial features such as steep-slope habitats (e.g. Lecours et al. 2017), or temporal features such as phytoplankton blooms (e.g. Bergkemper and Weisse 2018). Many spatial or temporal features that are critical drivers of regional biodiversity patterns can therefore be easily missed in global analyses where lower resolution environmental data are used.

6.3.3 Limitations in the statistical methods

Limitations in statistical methods can strongly influence biodiversity predictions. Reviewing the varying issues of the many different commonly used statistical methods is beyond the scope of this review. Here, we want to primarily focus on positive new developments. Nonetheless, we need to briefly mention a few important issues.

Statistical methods that do not account for the particular characteristics, biases and sampling artefacts of a dataset as listed in the section above can distort the inferences drawn, including detecting patterns where none exist (Warton et al. 2012, Warton et al. 2013, Foster et al. 2017). While some of these methods, such as dimension-reduction approaches based on distance metrics (e.g. Bray and Curtis 1957), have significantly contributed to our ecological understanding of the world, they were originally developed more than half a century ago when computational power was very limited. As such, the data needed to be simplified prior to the use of relatively simple, computational tractable analyses. Today, computational power is no longer a limitation, and more appropriate statistical tools are actively being developed for biodiversity analysis, including model-based methods that formally encapsulate assumptions, allow for predictions with uncertainty, facilitate model diagnostics and include robust validation procedures (Warton et al. 2015b).

6.4 A new era of biodiversity predictions

6.4.1 Biological and environmental data

In recent years, the biological and environmental data available for ecological analyses has increased dramatically (Fig. 6.1). Probably one of the most important developments regarding both biological and environmental data is that funding agencies and scientific journals now usually expect that data collected and/or used in the analysis will be made publicly available, and in particular be made findable, accessible, interoperable and reusable (FAIR principles) (Wilkinson et al. 2016). Global databases provide a platform for these widely shared data and provide easy access to biodiversity (e.g. Global Biodiversity Information Facility ‘GBIF’, Ocean Biogeographic Information System ‘OBIS’, World Register of Marine Species ‘WORMS’) and environmental data (e.g. General Bathymetric Chart of the Ocean ‘GEBCO’, Global Ocean Currents Database ‘GOCD’).

Not only do data generally become more available, but citizen science initiatives such as Reef-Life Survey (Edgar and Stuart-Smith 2014), Redmap (Pecl et al. 2014), and biodiversity games such as QuestaGame, now produce biological data at unprecedented spatial and temporal coverage (Dickinson et al. 2010), and at minimum cost. Although the data produced by these initiatives contain specific biases that need to be accounted for in their analysis, they have already helped to reveal new global hotspots of fish diversity (Stuart-Smith et al. 2013), identifying key features of marine protected areas (Edgar et al.

2014), and answering important questions regarding the impact of mass coral bleaching on reef-ecosystems (Stuart-Smith et al. 2018), the vulnerability of reef-fish to a warming ocean (Stuart-Smith et al. 2015) and geographic range-shifts in species (Sunday et al. 2015b). Further, automated processing of biological data can facilitate analysis of huge datasets while also reducing biases often inherent when using human observers, and consistent classification schemes such as CATAMI (Althaus et al. 2015) are being developed and applied to allow comparison of datasets from different regions.

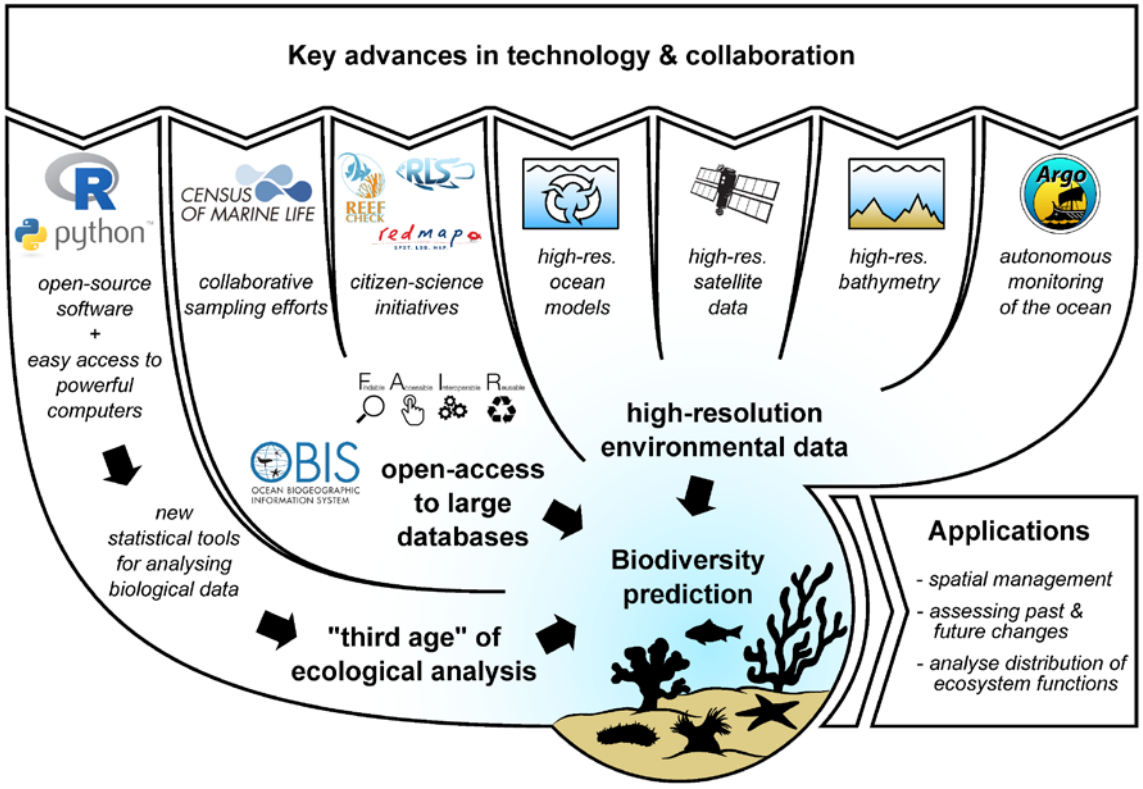


Figure 6.1: Overview of key advances in technology and collaboration that lead to improved biodiversity predictions. The 'third age' of ecological analysis refers to recently developed sophisticated hierarchical models that allow specifying joint statistical models (Warton et al. 2015a), as opposed to models of the second age that focus less on correlation between species (traditional species distribution models), and analysis of the first age that was developed under very limited technology (ordination techniques).

Increasing computing power and technical advances also mean environmental variables that are relevant for modelling the distribution of species can be sourced at higher spatial and temporal resolution than ever before. In particular, the frequency and quality of satellite observations are steadily increasing through the addition of higher-resolution or newly developed sensors such as cloud-penetrating synthetic aperture radar. Major advances in computing power and easy access to supercomputers allow developing ocean models with high spatial and temporal resolution that now regularly include simulations of tidal movements, eddy-kinetics, stokes drift, and ocean-ice-shelf interactions. Even at large scales covering entire oceans, models now exist at resolutions of 1 km (Stewart et al. 2018). These high-resolution ocean models, in combination with individual tracking of large particle numbers, allow generating previously unavailable but important environmental variables (e.g. availability of surface-derived food near the seafloor (Jansen et al. 2018a, Jansen et al. 2018c)), predict how larvae disperse (e.g. Brasier et al. 2017), or how species can break through oceanic barriers previously

thought impenetrable (Fraser et al. 2018). The data required to inform these models stem from an increasingly dense global networks of observing systems, such as ARGO-floats that regularly measure ocean-temperature and salinity (Riser et al. 2016), and can measure oxygen concentration, nitrate, chlorophyll, dissolved organic carbon and particle scattering if equipped with additional sensors (OAO 2018). Newly developed sail-drones aim to even take acoustic measurements of marine mammals and measure fish biomass in addition to measuring an entire suite of environmental parameters (Saildrone 2018). Improvements in the quantity, quality and the availability of biological and environmental data have paved the way to answer important biodiversity distribution questions at a wide range of scales and have stimulated developments in statistical methods to model these data.

6.4.2 Statistical methods

Analysing ecological data is difficult, mainly because of the high number of species and their sparsity (many zeros), the increasing dimensionality of covariates and the number of elements in any species-by-locations matrix. Modern approaches to ecological analyses leverage recent advances in computing power and in statistical and machine learning methodologies. This allows a step change in the way that ecological analysis can be approached. Instead of changing the data to suit the analysis, e.g. by deriving synthetic aggregate measures such as 'distance', it is now possible to design the statistical analysis to test hypotheses about the relationships between species and ecosystem dynamics, and fit models to the data.

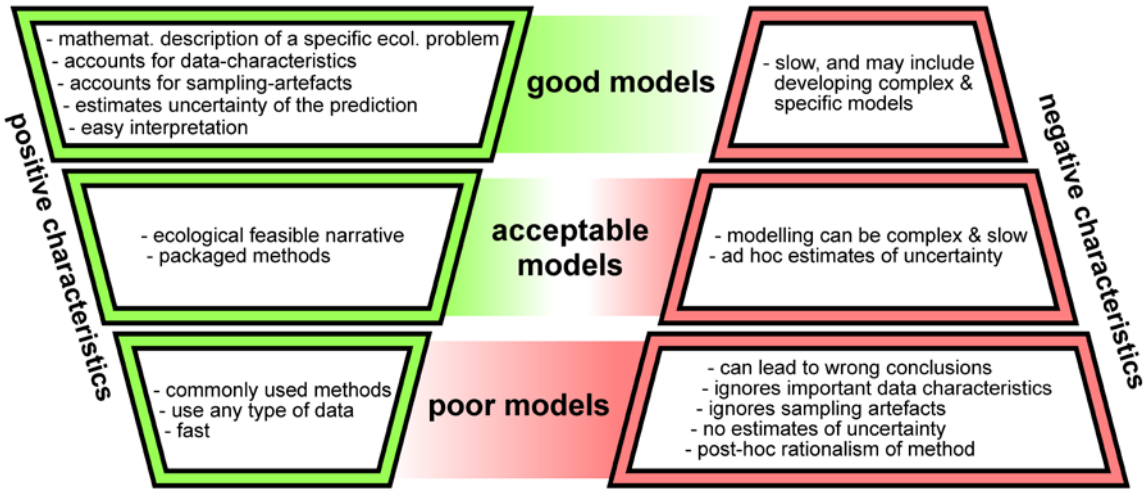


Figure 6.2: Overview of important positive and negative characteristics associated with different types of models for biodiversity prediction. 'Good' models make reliable and easily interpretable predictions that can take into account a wide range of data characteristics. Models falling under 'acceptable' can be suitable for analysis if the data has been collected without relevant sampling biases (e.g. by using a spatially and statistically balanced sampling design). Many commonly used methods for analysis fall under the 'poor' category because of how they transform complex multivariate data into univariate space.

Modern statistical methods for analysing ecological data change the models to suit the properties of the data (Warton et al. 2015b), and focus on the observed data directly rather than on arbitrary transformed or otherwise derived metrics. The result is statistical models that can predict the data, or some ecologically meaningful model-encapsulated quantity (such as a bioregion), while making

assumptions transparent (Warton et al. 2015b). Examples of this approach include combining species-specific models into a single hierarchical model (Ovaskainen and Soininen 2011), grouping species with similar responses to environmental factors into 'species archetypes' (Dunstan et al. 2011) or sites with similar characteristics into 'regions of common profile' (Foster et al. 2013), clustering matrix columns and rows of ordinal (Fernández et al. 2016) or binary and count data (Pledger and Arnold 2014), and accommodating the statistical properties of the data in unconstrained ordination (Hui et al. 2015). These approaches allow answering a wide range of ecological questions (Warton et al. 2015b, Ovaskainen et al. 2017), including how communities are distributed, structured or how they can change in the future (in their review, Ovaskainen et al. (2017) present a list of 10 topical questions that can be addressed).

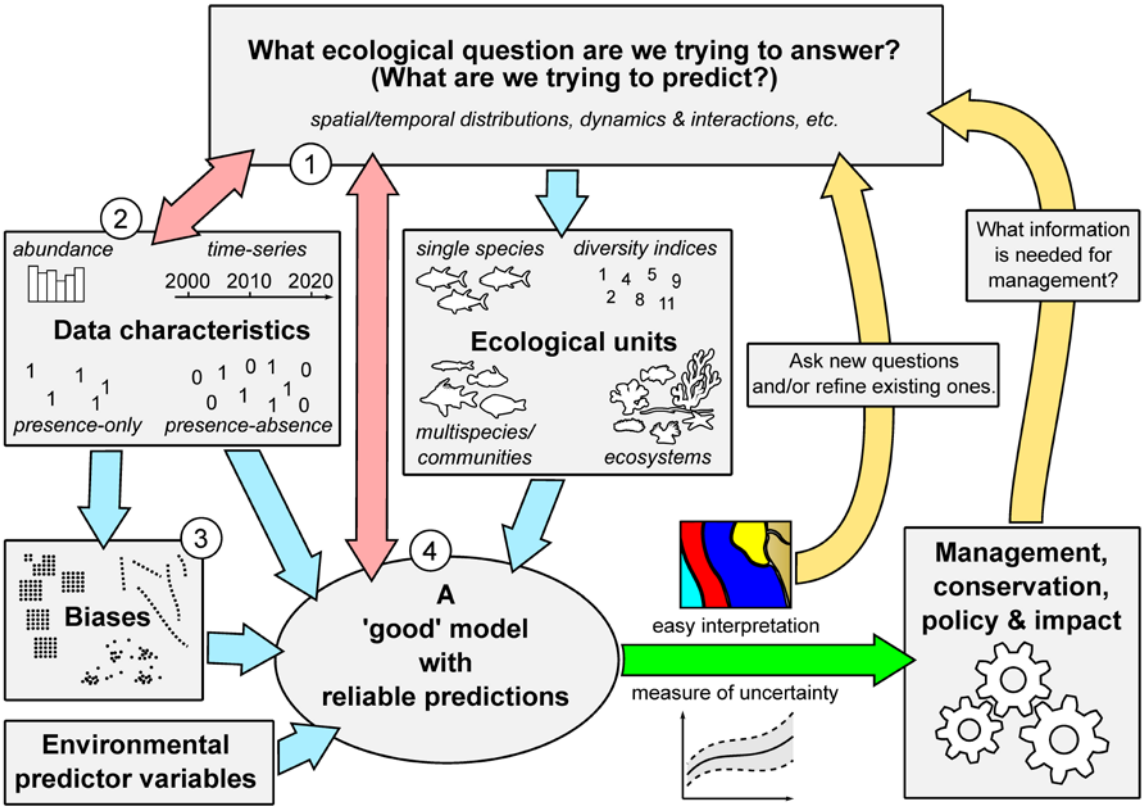


Figure 6.3: Overview of how a 'good' model can be used to address and refine important ecological questions and directly impact management, conservation and policy. **(1)** While traditionally ecological questions are asked before sampling occurs (first a question, then data collection, then analysis and finally results (e.g. Warton et al. 2015b)), this is usually not the case with global or large-scale analyses. In these analyses the kind of questions that can be asked depend on the characteristics of already collected data **(2)**, their biases **(3)** and the statistical tools available **(4)**. Therefore, the data and the statistical tools available influence/define what type of questions can be asked.

Although limitations exist even for these modern statistical methods, such as in analysing abundance data that contain many zeros and ones (see e.g. Chapter 5), in our opinion, one of the biggest current challenges is not technical but rather deciding what ecologically desirable predictions are required from the analysis, i.e. clarifying the ecological question(s) of interest. In this context, quantitative ecologists are already starting to push the boundaries of traditional research questions. An example is how traits are dispersed over the landscape (the so-called fourth-corner problem (Brown et al. 2014)), which is closely related to how molecular ecologists might query the spatial pattern of molecular

markers (e.g. Hanks et al. 2016). These are just some examples of how statistical methods can be developed to address particular ecological needs, once those needs are succinctly expressed.

There will never be a single analysis strategy that can address all present and all future research questions and associated problems. Ensuring that the methods applied are appropriate to the data and the ecological questions of interest is key. Are the assumptions the model makes and its structure answering the question of interest? Often novel research questions will require novel analytical solutions, and sequentially applying multiple existing methods makes assessment of uncertainty more complex and scientific inference more ambiguous. It is important that current and especially future researchers are armed with intuitive understanding of statistical thinking rather than be given a set of standard tools for analysis (that may well soon be outdated). Based on this argument, we define the characteristics of three different model-types that researchers choose from: A 'good' model, an 'acceptable' model, and a 'poor' model (Fig. 6.2).

- A good model mathematically describes a specific ecological problem, ranging from simple linear regressions for normally distributed data to highly sophisticated analyses for multi-species data with particular data-characteristics and sampling-biases. Importantly, the output from a good model contains an estimate of uncertainty of the prediction and is readily interpretable so that important information can be easily communicated to managers and stakeholders (Fig. 6.3).
- An acceptable model would usually not be capable of taking into account specific sampling-biases but can be appropriate to use if the data have been collected thoroughly, e.g. using a spatially and statistically balanced sampling design.
- In contrast to 'good' and 'acceptable' models, a poor model modifies the data to suit an analytical technique, rather than designing the model to describe the data. Analysing modified data can lead to misleading conclusions about various aspect of the ecosystem with potentially detrimental outcomes for conservation where management decisions are based on these results.

6.5 How will we predict biodiversity in the future?

The recent developments outlined above not only improve predicting the distribution of biodiversity, but they also open new ways of how to investigate species, communities and ecosystems. It has been suggested that ecological analysis recently entered the 'third age' (Warton et al. 2015a) marked by the advent of sophisticated statistical models that allow analysing complex multi-variate ecological data while accounting for specific data characteristics and sampling biases. To deliver robust ecosystem-assessments these approaches need to be broadly implemented, and then linked to dynamic process models. An integrated approach that combines the strengths of statistical models (particularly estimating uncertainty and accounting for data-characteristics and biases) with dynamic process models will be challenging to develop, but has the potential to reveal more insight into an ecosystem than the sum of the individual approaches. As an example, in Chapter 5 we show how a combined assessment of the spatial distribution and structural dynamics of deep benthic Antarctic marine communities can be used to assess the influence of potential futures on this community that otherwise would not be possible. Integrated assessments would allow addressing new and more complex

ecological questions in both little studied and well understood regions. Potential questions include (i) *where*, *when* and *how* species communities will restructure with climate change, and (ii) *where*, *when* and *how* this affects biodiversity and important ecosystem services, taking into account interspecies interactions, dispersal rates, reproductive cycles and other important factors not normally included in species distribution models.

The recent and imminent technical advances can also change the way scientific advice is communicated to managers and stakeholders. Predictions that are easy to interpret and carry a message about their uncertainty are set to become an integral part of decision processes for managing and conserving marine biodiversity, just as is already the case in fisheries where catch quota are set with respect to probabilities of population collapse and recovery (although care needs to be taken because models can be misused (Dickey-Collas et al. 2014)). Communicating uncertainty in the predictions is particularly relevant where large investments are considered, such as for the AICHI target to protect 10% of the world's oceans. Knowing whether there is a 0, 10, 50 or 100 per cent chance of losing/gaining certain species/communities depending on policy and management and conservation decisions is invaluable to assess policy impact.

6.6 Conclusion

Biodiversity from local to global scales can now be assessed and predicted as never before. We are at this point of step-change of biodiversity prediction because (i) new observing technologies (and the rising distribution of existing ones) allow obtaining unprecedented data of biological systems and environmental conditions, (ii) much of these data are findable, accessible, interoperable and reusable, (iii) new statistical methods are available for relating biological samples to environmental data in ways that models are easily interpretable and contain estimates of uncertainty for the predictions, (iv) access to powerful computers enable full use of these advances and (v) integrating biodiversity predictions with dynamical process models of communities allow new questions to be asked, such as how ecosystems are structured and how they change spatially and through time.

Ecologists today can take full advantage of the wide range of recent technical developments and should question using those analytical methods that fail to capture and express the uncertainty of predictions. Although modern statistical methods can be more challenging to use than many traditional analytical approaches, statistical methods that fit models to the data should be widely adopted as a benchmark for predicting biodiversity. Predicting biodiversity in a way that results are readily interpretable and key messages are well communicated helps to improve the decision cycle and improve management and conservation outcomes, a top priority in light of the current unprecedented biodiversity loss.

Future analyses of biodiversity should consider combining statistical and dynamic process models into integrated approaches that will allow a more complete understanding of how spatial, temporal and ecological interactions and feedbacks in the ecosystem affect its structure and functioning. Developing frameworks that combine the advantages of the respective methods will be challenging, but will help to understand where, when and how changes might occur, and to give confidence to management decisions for the mutual benefit of marine ecosystems and humanity.

Conclusion

This thesis has developed, applied and discussed new approaches to map the spatial, temporal and structural distribution of marine biodiversity. The key findings of this thesis are:

- Food-availability at the Antarctic seafloor below the photosynthesis zone can be estimated using satellites, ocean models and particle-tracking, and directly relates to the abundance and species richness of key Antarctic seafloor fauna. The linkage between the ocean-surface and the seafloor is therefore considered to be relatively direct in the Antarctic. As a result, changes in the icescape, such as the calving of the Mertz Glacier Tongue in 2010, can strongly affect seafloor communities through changes in seafloor food-availability and regional differences in suspension feeder abundances are predicted to emerge on the George V shelf in East Antarctica.

- Environmental conditions, including seafloor food-availability, explain much of the variation in the distribution of benthic macro-invertebrates and demersal fish on the East Antarctic continental shelf. This stands in contrast to many previous Antarctic studies that have found little consistency in the relationship between the environment and the seafloor fauna. A major factor that influences how biodiversity patterns relate to differences in the environment is how the data are analysed. Grouping species by taxonomic and functional similarity amalgamates species with different responses to environmental conditions, and therefore distorts the predicted spatial patterns in biodiversity, reduces confidence in the predictions and inhibits detecting potentially important biodiversity patterns.

- Combining species distribution models with a dynamic network model into an integrated approach allows analysing and validating spatial patterns in the distribution and variation of seafloor communities. Assemblages of demersal fish and benthic macro-invertebrates on the East Antarctic continental shelf show relatively similar spatial distributions. Our results suggest four main habitats that are commonly found in marine ecosystems globally, namely shallow-flat, shallow-steep, deep-flat and deep-steep. The dynamic network model suggests that no major changes in benthic community structure will occur in this region as result of increased primary production in the future.

- A number of recent technical developments, including the developments made in this thesis, suggest that we are at a point of step-change in the way spatial, temporal and structural patterns of biodiversity can be predicted. Key to improve management and conservation outcomes are reliable and easily interpretable biodiversity predictions that include estimates of uncertainty.

The key findings in this thesis highlight how interdisciplinary studies and novel analytical approaches help to better understand the ecology of the unique and biodiverse Antarctic ecosystem. The food-availability models (Chapters 2 & 3) and the integrated approach of assessing the distribution and variation of species communities (Chapter 5) allow insights into how Antarctic species abundances and community structure might change even when no time-series of biological data are available.

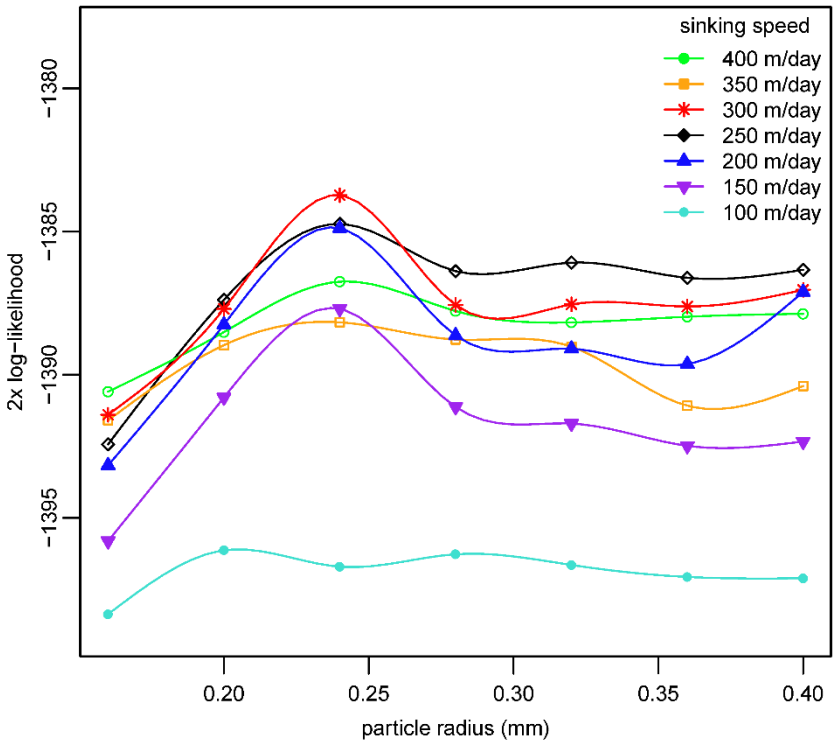
Modern statistical methods, such as the Species Archetype Models used in this thesis (Chapters 4 & 5), allow detailed and reliable predictions of seafloor biodiversity, and add to a number of important other recent developments (Chapter 6) that mark significant improvements with regard to how the spatial, temporal and structural patterns of biodiversity can be predicted and how this information can be communicated to decision makers. Reliable and easily interpretable information about biodiversity patterns can be used as context for future monitoring and assessment of the ecosystem, and can be used to more accurately assess the representativeness of current and future planned marine protected areas. Further, the advances help to understand how climate change can affect the seafloor in the future and evaluate the robustness of marine protected areas against future changes in the Southern Ocean.

In conclusion, this thesis increases understanding of how the ocean-surface is linked to the Antarctic seafloor, and develops techniques to more confidently map spatial, temporal and structural patterns of seafloor biodiversity where sampling is difficult and costly. These advances are highly relevant in light of climate change, the current unprecedented loss of biodiversity and the vastness of the global oceans.

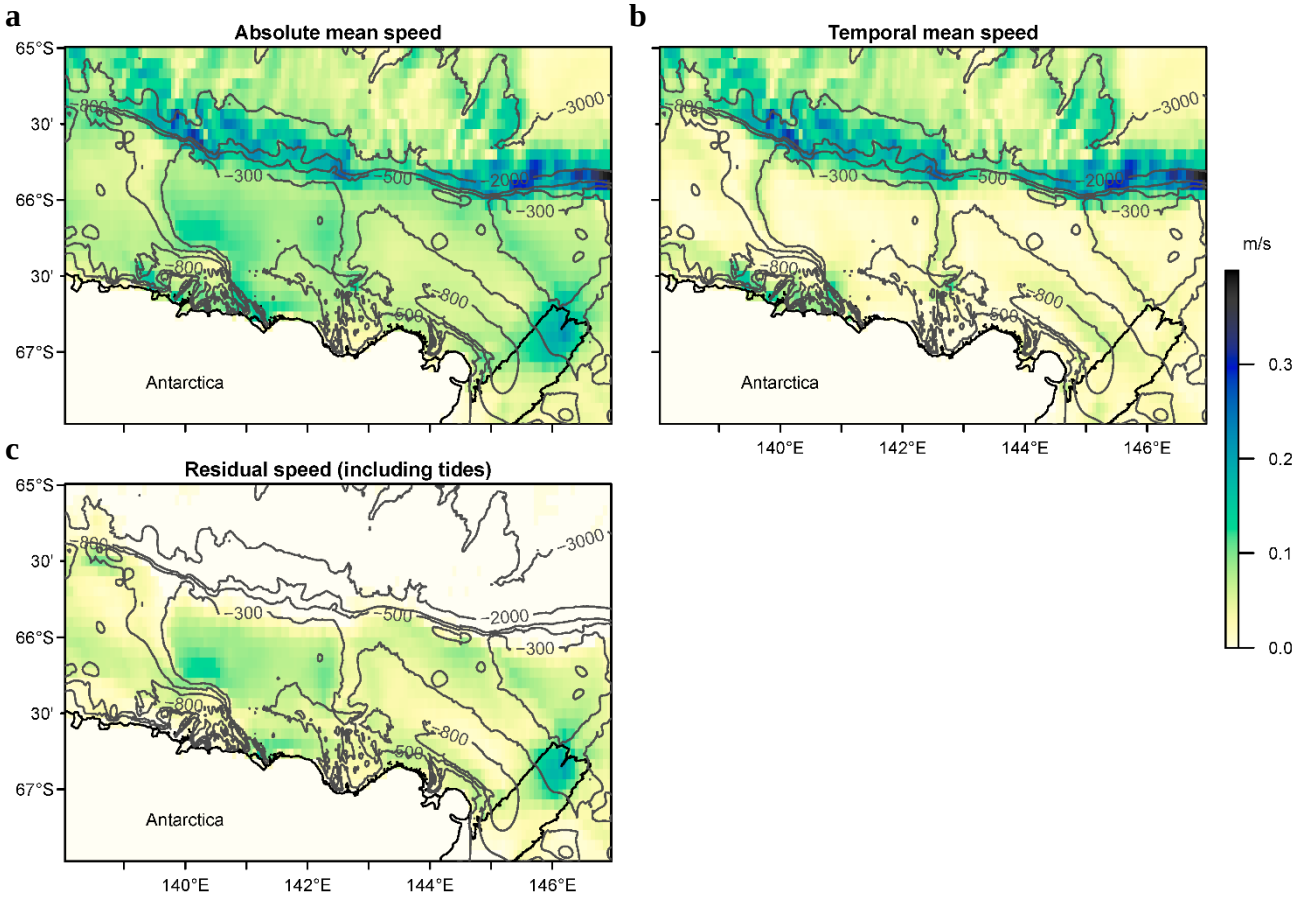
Appendix A

Supporting Information for Chapter 2

Appendix A Figure 1: Statistical fit of the settling-model given different radius of particle sizes used in the settling-model. The statistical fit is measured using 2x log-likelihood, and only a selected range of values close to the best fitting particle size are presented. Each line/colour represents one of seven different particle sinking-speeds used in the sinking-model. The settling-model uses the output from the sinking-model as its input, therefore the results of the settling-model partially depend on the sinking-model. Higher values of the 2x log-likelihood represent a better fit of the model. The best statistical fit of the settling-model occurred at a particle radius of 0.24 mm, combined with the input from a sinking-model run with 300 m/day sinking speed.

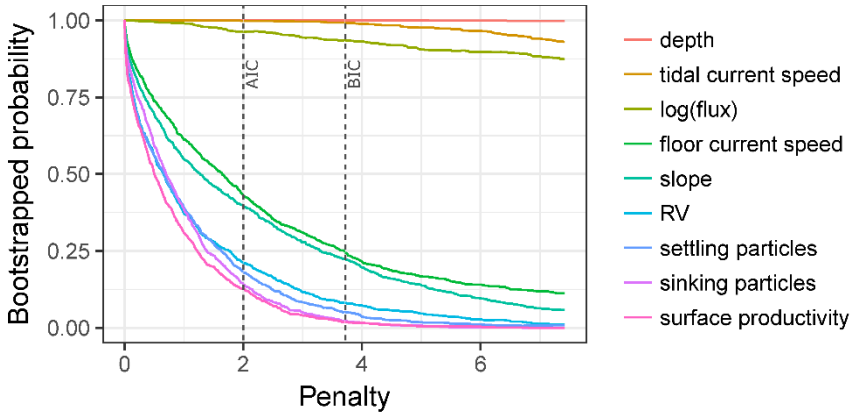


Appendix A Figure 2: Seafloor current speeds derived from a regional ocean model(Cougnon et al. 2013) for the study region. **a**) absolute mean current speed, **b**) temporal mean current speed, and **c**) residual current speed which indicates tide-affected areas in particular. Noteworthy are the high speeds of currents moving in one direction along the shelf-break at around 65.5°S. Currents between the shelf-break and the coast are very low on average (centre plot) with the exception of some particular sites. Current speed on the shelf is mainly attributable to tidal currents, as shown in the bottom plot.

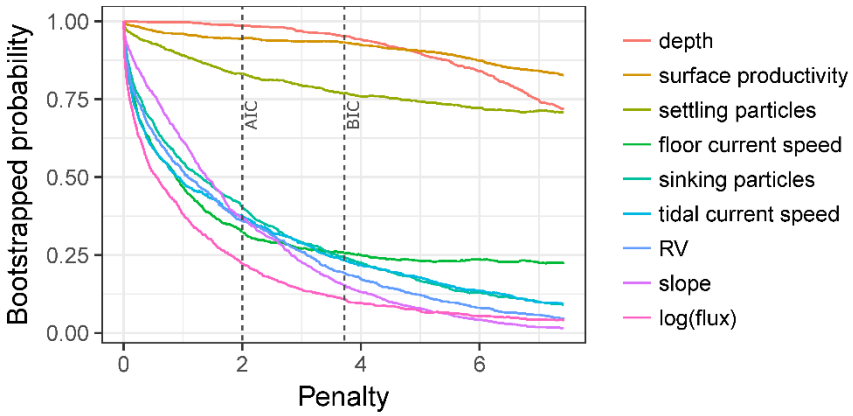


Appendix A Figure 3: Variable inclusion plot. This plot shows the probability of covariates being selected in the final regression model when a stepwise selection of model terms is applied to 1,000 bootstrap replicates of the data. The probability of variable selection is shown as a function of the penalty multiplier on the number of estimated parameters, with Akaike Information Criterion (AIC) at penalty=2 and Bayesian Information Criterion (BIC) at penalty=log(n) where n is the number of observations. Variables with high values in bootstrapped probability at the AIC and BIC marks are more robust predictors of functional group percentage cover across the region than variables with low values. A random variable (RV) is included in the analysis as reference to aid in interpretation.

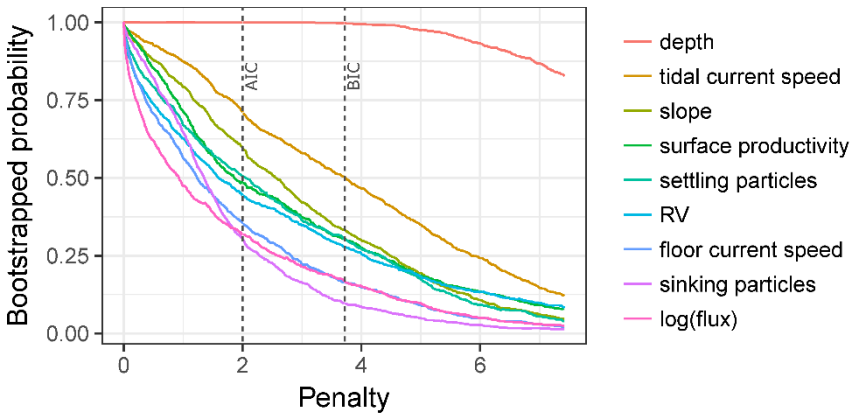
a Suspension feeders



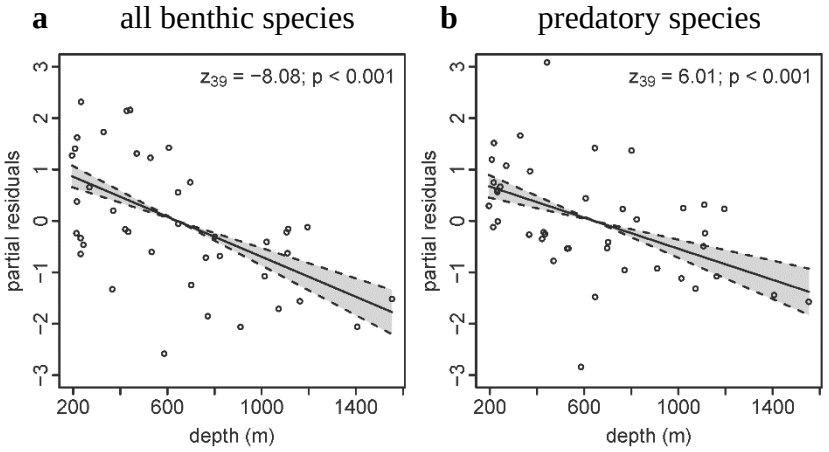
b Deposit feeders



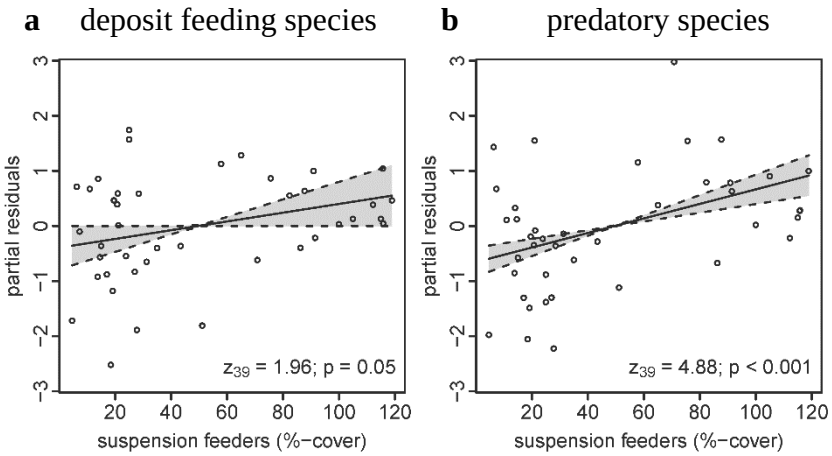
c Predators



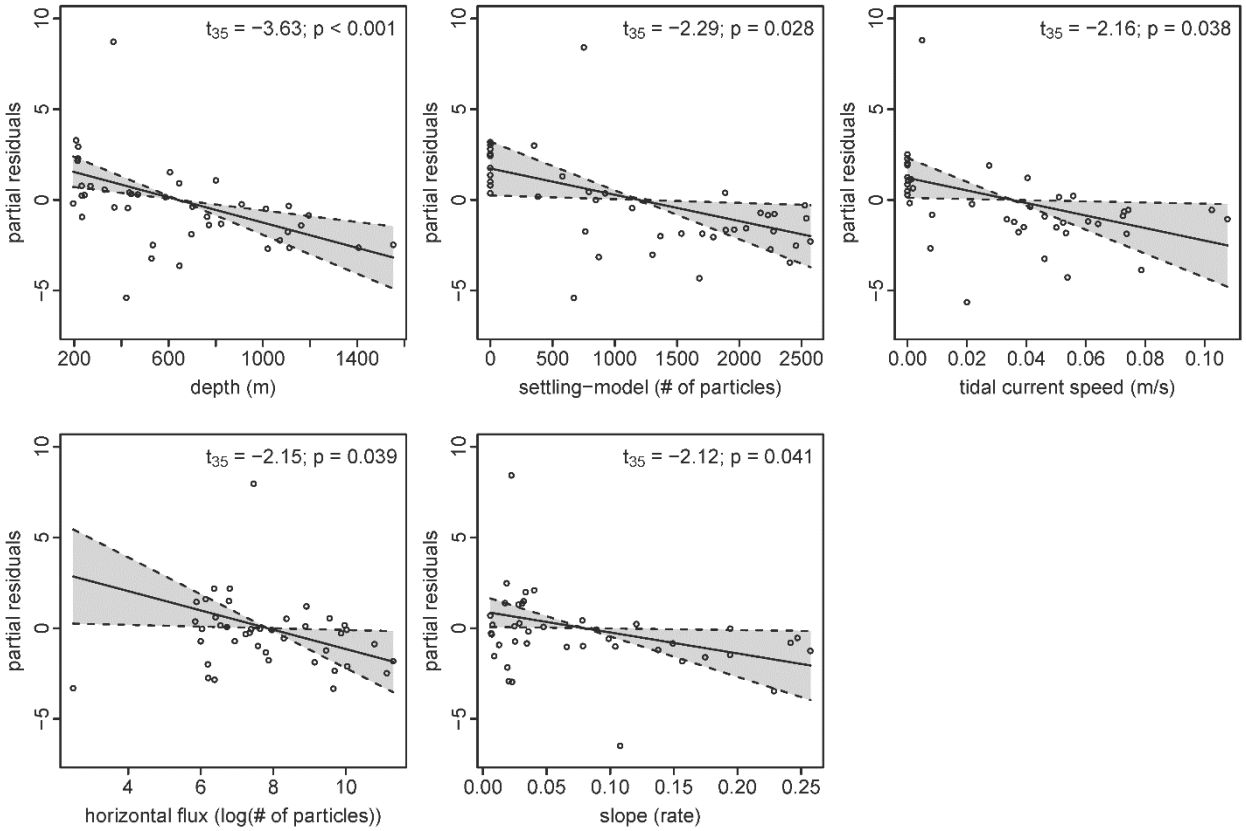
Appendix A Figure 4: Species richness vs. environmental variables. Partial residual plots for the relationship between depth and the number of **a**) all benthic species (%-deviance explained = 55.7) and **b**) predatory species (%-deviance explained = 49.4). Depth is the only variables remaining after a stepwise removal of non-significant terms in the multiple linear regression analysis. An offset-term is included in the analysis to correct for the number of pictures taken at each of the 41 sites. The shaded areas mark the 95 % confidence intervals of the estimated mean.



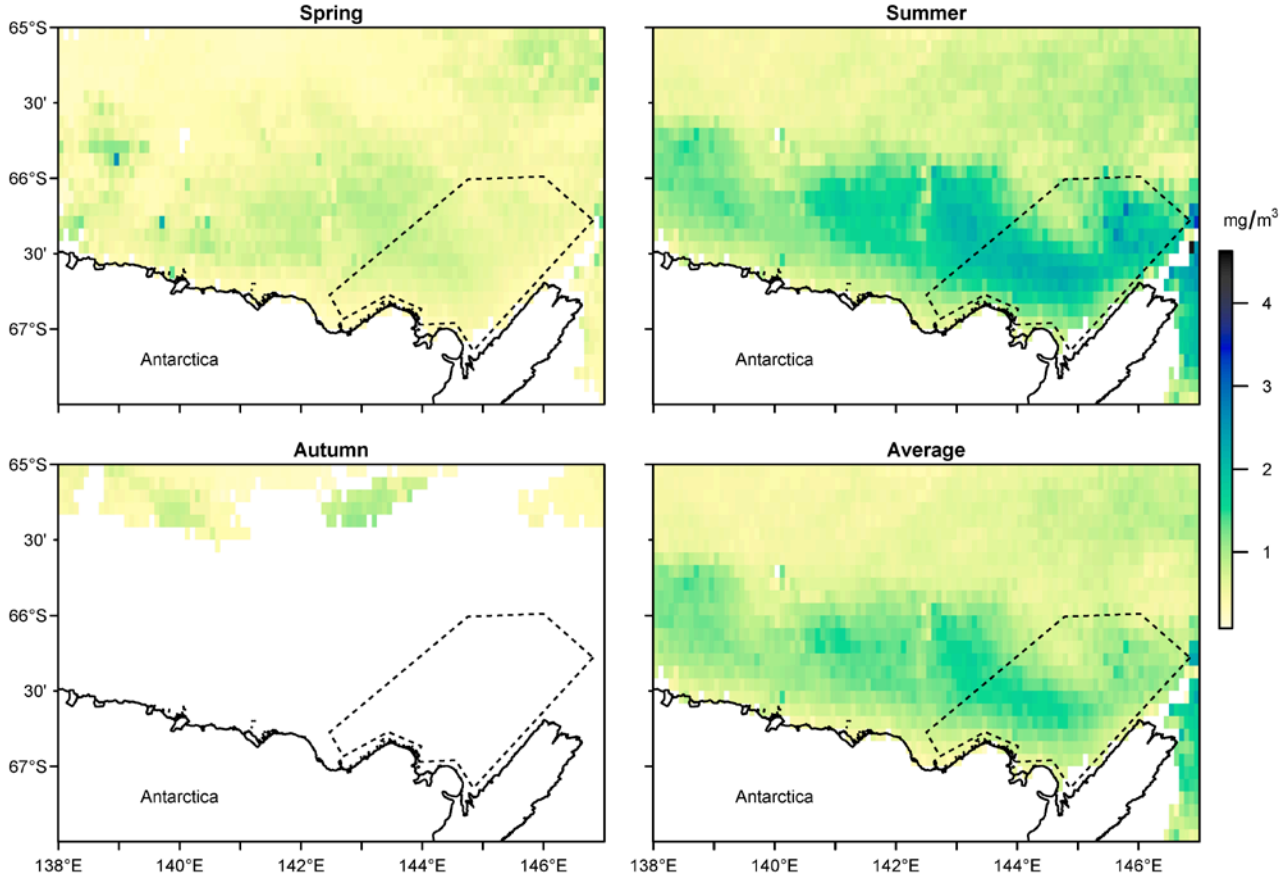
Appendix A Figure 5: Species richness vs suspension feeder abundance. Partial residual plot showing the relationship between suspension feeder cover and **a**) number of deposit feeding species observed (%-deviance explained by model = 9.1), and **b**) number of predatory species observed (%-deviance explained by model = 35.2). An offset-term is included in the negative binomial regression analysis to correct for the number of pictures taken at each of the 41 sites. The shaded areas mark the 95 % confidence intervals of the estimated mean.



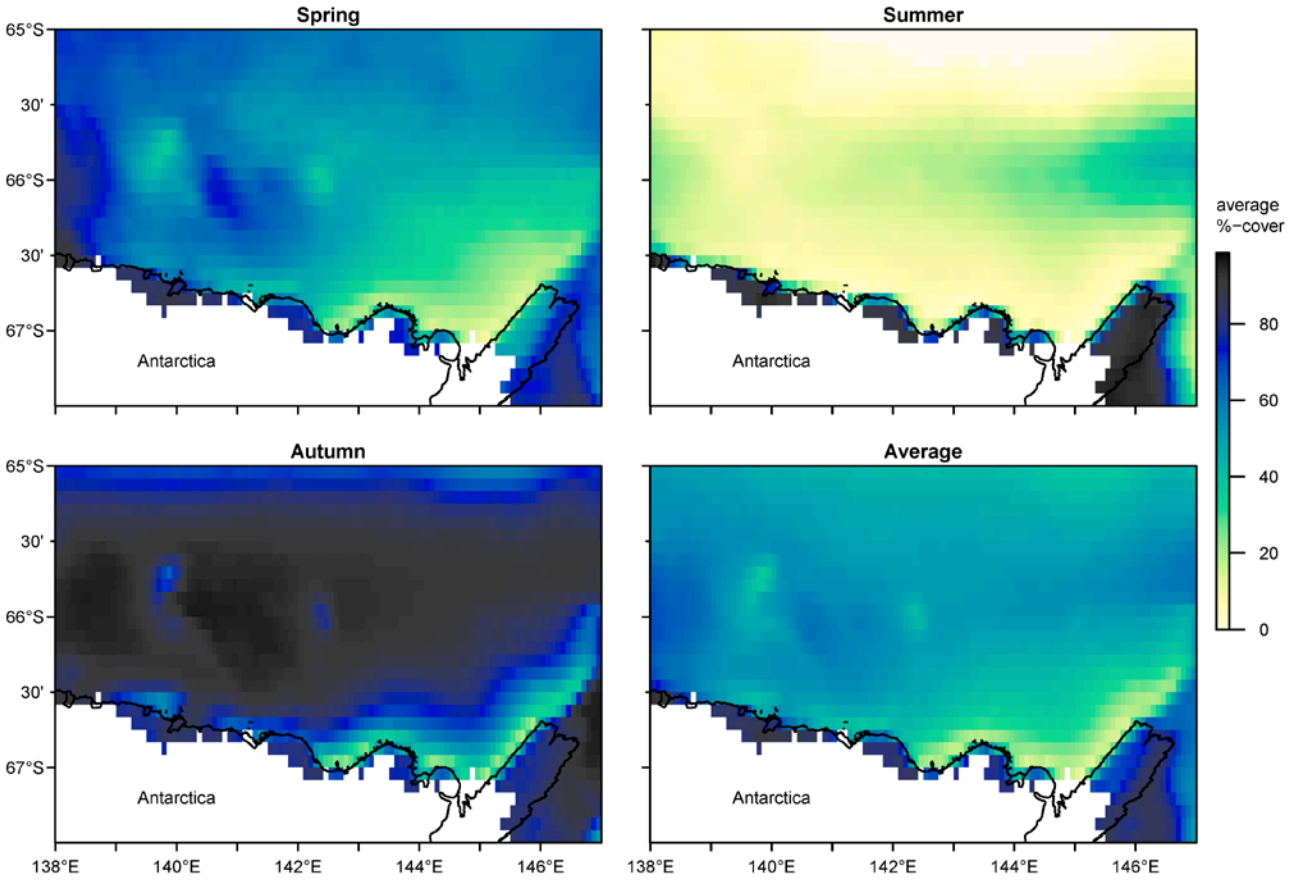
Appendix A Figure 6: Predator abundance vs. environmental variables. Partial residual plots for the relationship between selected environmental variables and the percent cover of predators (adjusted-R^2= 0.318). Only environmental variables marked as significant in the weighted multiple linear regression analysis are shown. Data points are weighted by the number of images taken at each of the 41 sites. The shaded areas mark the 95 % confidence intervals of the estimated mean.



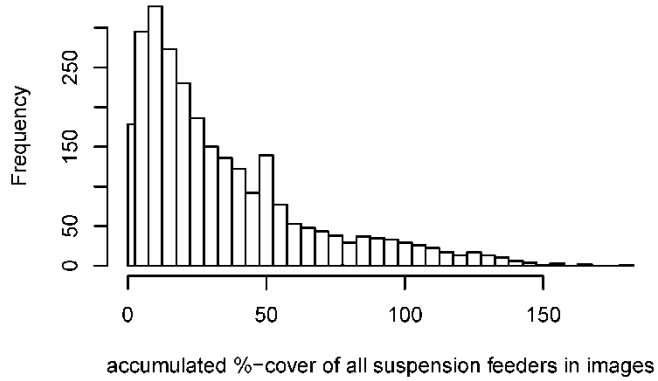
Appendix A Figure 7: Satellite derived(NASA Goddard Space Flight Center 2014), corrected(Johnson et al. 2013) estimates of surface chlorophyll-*a* concentrations in different southern hemisphere seasons. The dashed line marks the outline of the largely ice-free waters of the Mertz Polynya(Campagne et al. 2015). There are no observations for winter, when the region is covered in ice and receives little to no sunlight.

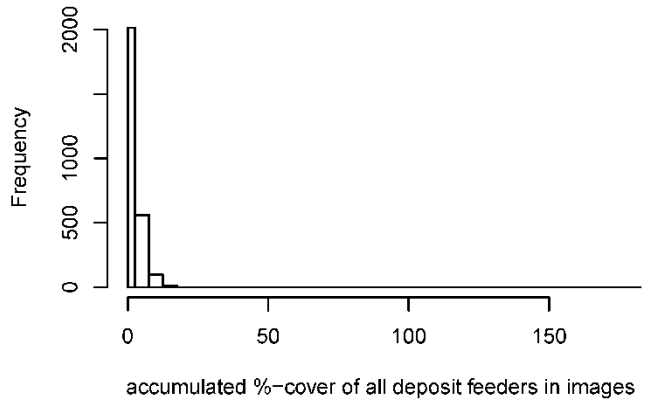


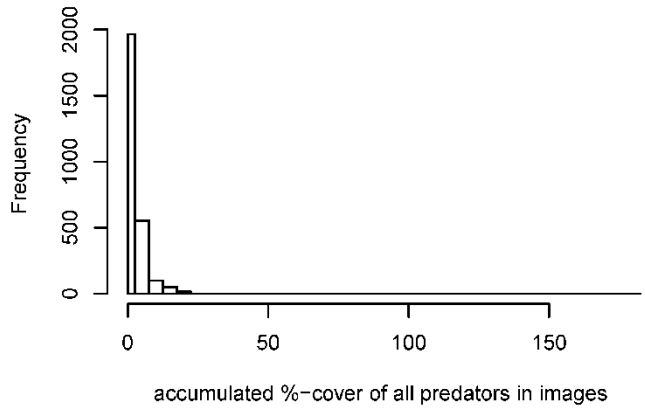
Appendix A Figure 8: Satellite derived(NASA Goddard Space Flight Center 2014) estimates of the percentage of sea ice cover in different southern hemisphere seasons. There are no observations for winter, when satellites cannot obtain measures of reflectance due to missing sunlight.



Appendix A Figure 9: Analysis of the frequency of observed percentage cover in the epibenthic imagery (2685 images). Values were scored in 5 percent bins from 0-50 %, and 10 percent bins from 50-100 %. Accumulated percent-cover can reach values higher than 100% when multiple species overlap within a picture.







Appendix A Table 1: Faunal abundances. Results from weighted multiple linear regressions with model terms selected by Akaike Information Criterion (AIC) and consecutive removal of non-significant terms. **a**) suspension feeder cover in relation to depth, horizontal flux of particles (=log(flux)) and tidal current speed (adjusted-R^2= 0.677). **b**) cover of deposit feeders in relation to depth, sinking particles from the sinking model and floor current speed (adjusted-R^2= 0.718). **c**) cover of predators in relation to depth, settling particles, tidal current speed, horizontal flux of particles and slope of the seafloor (adjusted-R^2= 0.318).

a

model terms	Estimate	Std. error	t value	p-estimate
Intercept	-16.7	15.9	-1.054	0.299
depth	-0.060	0.008	-7.692	< 0.001
log(flux)	10.5	1.8	5.742	< 0.001
tidal current speed	546	119	4.579	< 0.001

b

model terms	Estimate	Std. error	t value	p-estimate
Intercept	3.42	0.46	7.364	< 0.001
depth	-0.00128	0.00040	-3.183	< 0.001
settling particles	0.00184	0.00027	-6.778	< 0.001
surface productivity	-0.00104	0.00016	-6.594	< 0.001

c

model terms	Estimate	Std. error	t value	p-estimate
Intercept	1.23	0.29	4.281	< 0.001
depth	-0.000349	0.000096	-3.633	< 0.001
settling particles	-0.000150	0.000063	-2.286	0.028
tidal current speed	-3.46	1.60	-2.160	0.038
log(flux)	-0.0533	0.0248	-2.150	0.039
slope	-1.16	0.55	-2.120	0.041

Appendix A Table 2: Faunal abundances. Analysis of Deviance table for the stepwise backward selection of model terms. Presented are the changes in Akaike Information Criterion (AIC) as a result of simplifying the model of **a**) the suspension feeders and **b**) the deposit feeders and **c**) predators. We further removed the non-significant term floor current speed from the suspension feeder model. Df = degrees of freedom.

a

model step	deviance	Df	residual deviance	AIC
full model		32	543210	407.16
- settling particles	2098	33	545308	405.32
- sinking particles	6634	34	551942	403.81
- surface productivity	1778	35	553720	401.94
- slope	8616	36	562336	400.58
- floor current speed	29312	37	591648	400.66

b

model step	deviance	Df	residual deviance	AIC
full model		32	1219	157.08
- log(flux)	2.10	33	1221	155.15
- tidal current speed	9.35	34	1230	153.46
- slope	49.4	35	1280	153.07
- sinking particles	58.6	36	1338	152.91
- floor current speed	59.6	37	1398	152.69

c

model step	deviance	Df	residual deviance	AIC
full model		32	6985	228.66
- floor current speed	189.7	33	7175	227.76
- sinking particles	215.8	34	7391	226.97
- surface productivity	22.5	35	7413	225.10

Appendix A Table 3: Species richness. Results from negative binomial regressions with model terms selected by Akaike Information Criterion (AIC) and consecutive removal of non-significant terms. The model contains an offset in the form of log(number of images) to account for sampling effort. **a**) suspension feeder richness in relation to depth, settling and sinking particles (deviance explained = 58.9 %). **b**) richness of deposit feeders in relation to depth and log(flux) (deviance explained = 46.9 %). **c**) richness of predators in relation to depth (deviance explained = 49.4 %)

a

model terms	Estimate	Std. error	t value	p-estimate
Intercept	0.362	0.380	0.951	0.342
depth	-0.00194	0.00029	-6.727	< 0.001
settling particles	-0.000407	0.000180	-2.234	0.026
sinking particles	0.000317	0.000125	2.532	0.011

b

model terms	Estimate	Std. error	t value	p-estimate
Intercept	-0.833	0.580	-1.436	0.151
depth	-0.00118	0.00039	-3.034	0.002
log(flux)	-0.201	0.075	-2.692	0.007

c

model terms	Estimate	Std. error	t value	p-estimate
Intercept	-1.27	0.19	-6.723	< 0.001
depth	-0.00151	0.00025	-6.005	< 0.001

Appendix A Table 4: Species richness. Analysis of Deviance table for the stepwise backward selection of model terms. Presented are the changes in Akaike Information Criterion (AIC) as a result of simplifying the model of **a**) the suspension feeders, **b**) the deposit feeders and **c**) predators. We further removed the non-significant terms tidal current speed and slope from the suspension feeder model, and tidal current speed from the deposit feeder model. Df = degrees of freedom, n.a. = not available.

a

model step	deviance	Df	residual deviance	AIC
full model		32	45.24	328.41
- surface productivity	0.318	33	45.56	326.68
- floor current speed	0.845	34	46.40	325.93
- log(flux)	0.0368	35	46.44	325.04
- tidal current speed	n.a.	36	n.a.	326.23
- slope	n.a.	37	46.46	326.58

b

model step	deviance	Df	residual deviance	AIC
full model		32	28.06	144.41
- floor current speed	0.0177	33	28.08	142.46
- slope	0.330	34	28.41	140.54
- surface productivity	0.223	35	28.18	138.59
- tidal current speed	0.251	36	27.93	136.69
- settling particles	0.537	37	27.39	135.62
- sinking particles	0.550	37	26.85	135.49

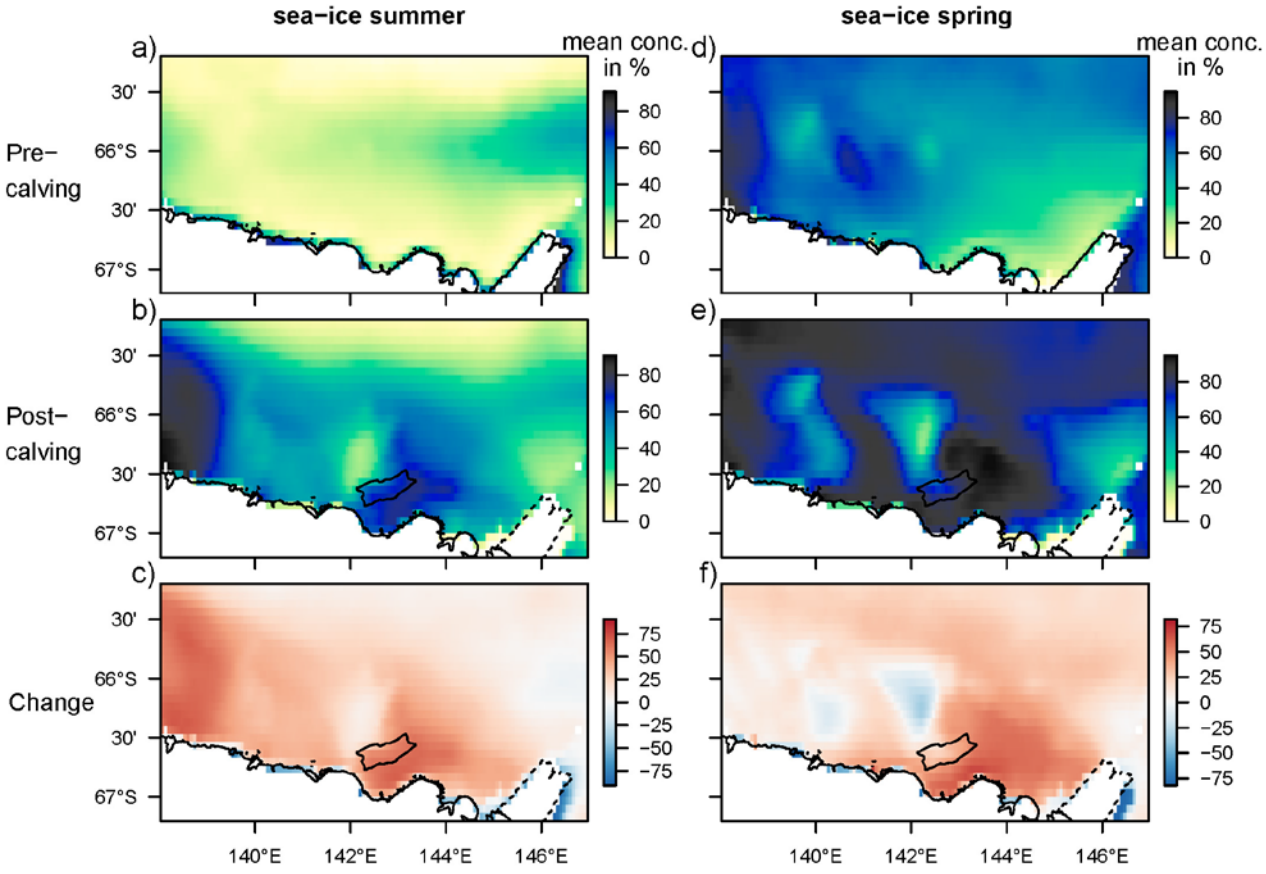
c

model step	deviance	Df	residual deviance	AIC
full model		32	37.51	188.28
- slope	0.321	33	37.83	186.31
- settling particles	0.559	34	37.27	184.52
- sinking particles	0.870	35	36.40	183.27
- log(flux)	0.982	36	37.39	181.91
- surface productivity	0.617	37	36.77	181.68
- floor current speed	0.999	38	37.77	181.33
- tidal current speed	1.27	39	36.50	180.31

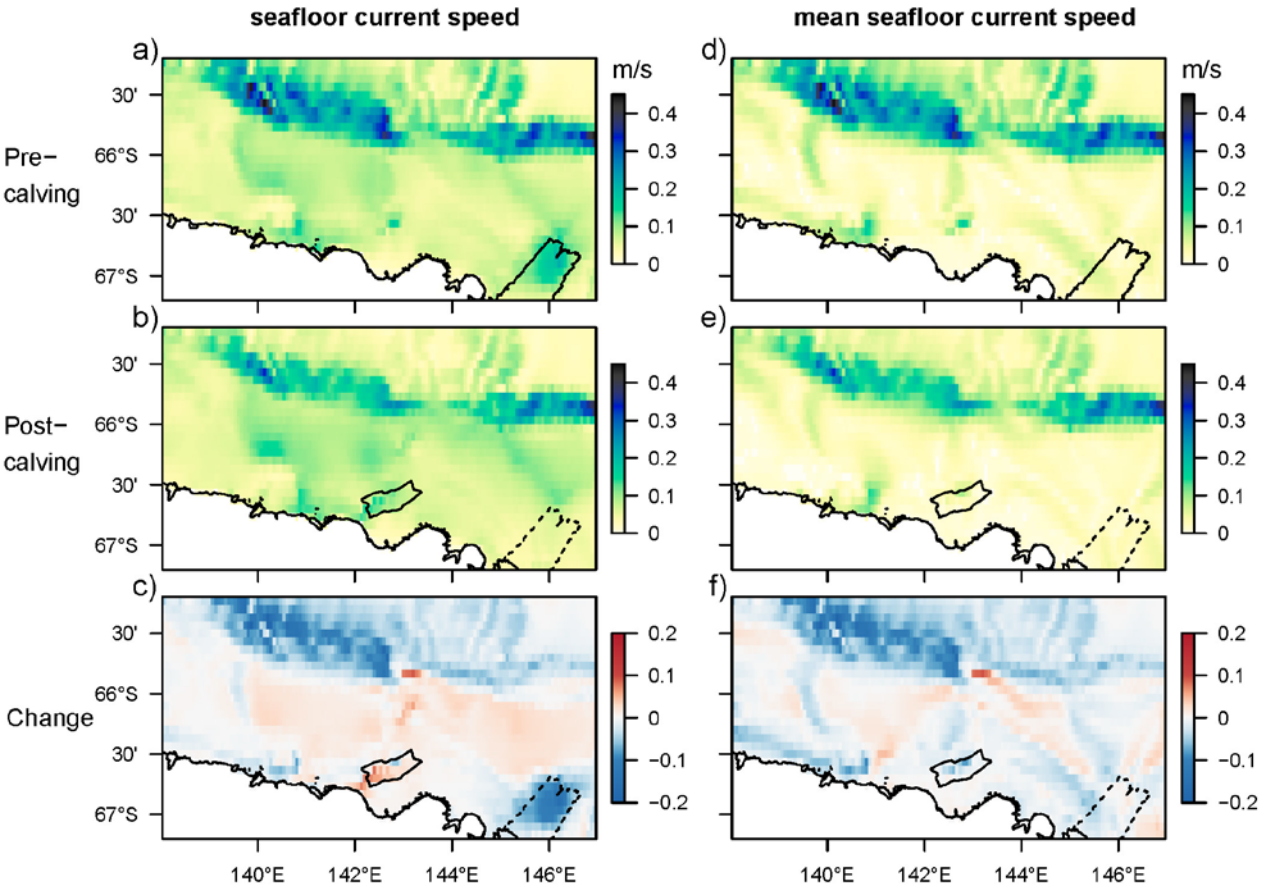
Appendix B

Supporting information for Chapter 3

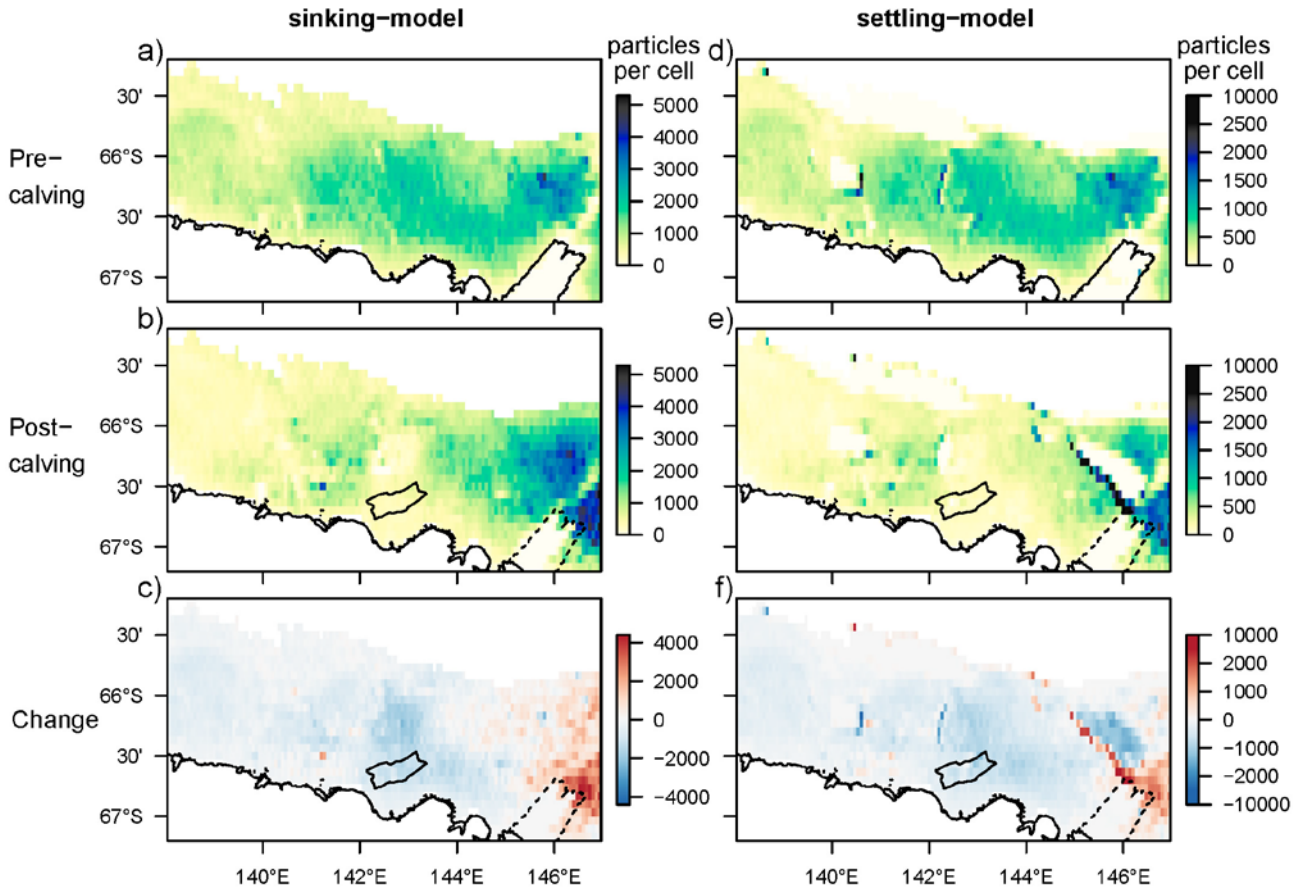
Appendix B Figure 1: Satellite derived measures (Cavalieri et al. 1996 , updated yearly) of average sea-ice concentration for pre- and post-calving in summer **a**-**c**) and in spring **d**-**f**).



Appendix B Figure 2: Seafloor current speeds obtained from a regional ocean model for pre- and post calving (Cougnon et al. 2017). **a-c**) are absolute current speed at the bottom layer of the model. **d-f**) show the numeric mean speed of the currents (absolute current speed minus tidal current speed (Fig. 3.3)).



Appendix B Figure 3: Food-availability-model (FAM) results for pre- and post calving conditions. **a-c**) are results from the sinking-model, showing the relative number of particles arriving near/ or settling temporarily on the seafloor. **d-f**) shows the number of particles permanently settling on the seafloor. Note how changes between pre- and post-calving resemble the changes in surface chlorophyll-*a* (Fig. 3.3).



Appendix B Table 1: Results from stepwise backwards selected multiple negative binomial regression with model terms selected by Akaike Information Criterion (AIC). We used the environmental predictor variables identified as important in Jansen et al. (2018c) to generate the full model (depth, tidal current speed and horizontal flux). Only depth and horizontal flux are selected as important variables (adjusted proportion of deviance explained = 0.443).

model terms	Estimate	Std. error	z value
Intercept	8.90	0.31	29.13
depth	0.00180	0.00024	7.52
log(flux)	0.0870	0.0467	1.86

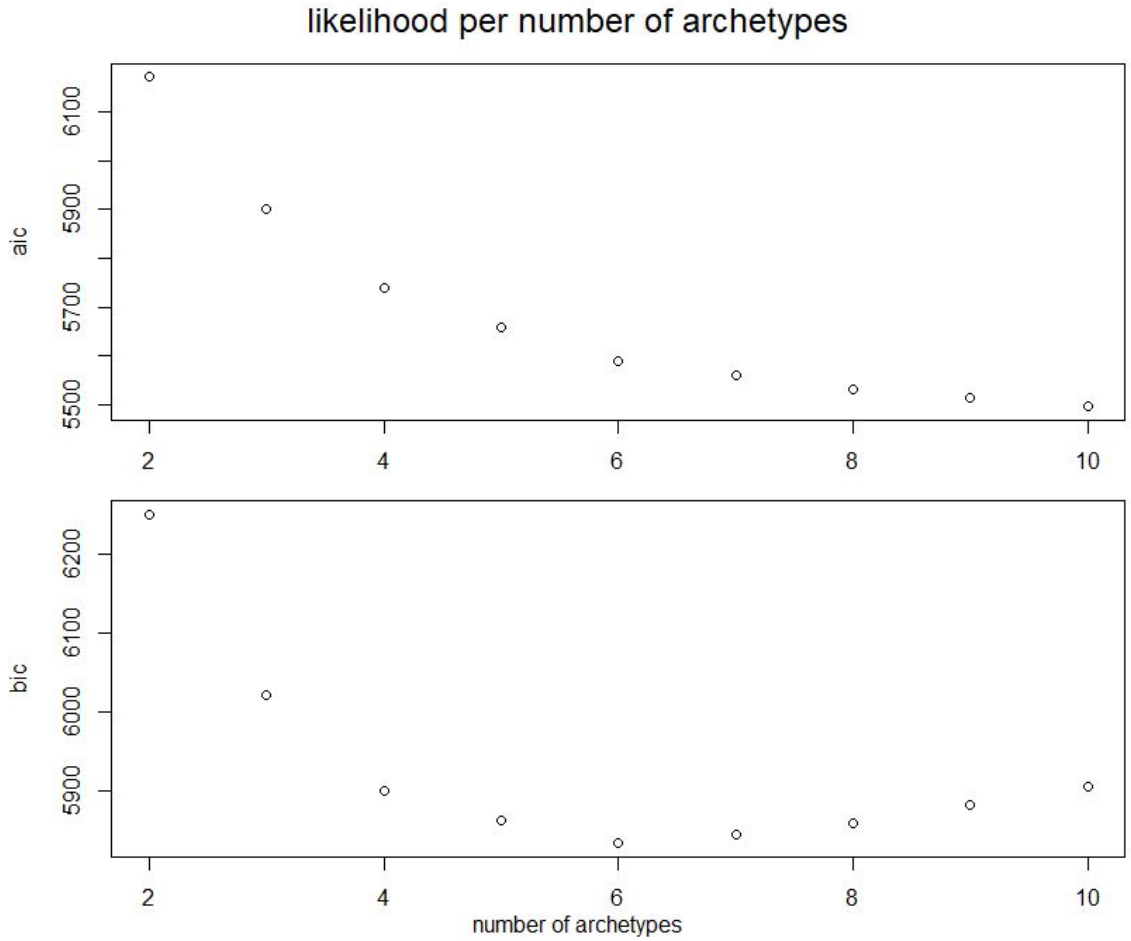
Appendix B Table 2: Analysis of Deviance table for the stepwise backward selection of model terms. Presented are the changes in Akaike Information Criterion (AIC) as a result of removing the term tidal current speed from the model of suspension feeder abundance. Df = degrees of freedom.

model step	deviance	Df	residual deviance	AIC
full model		37	42.93	745.67
- tidal current speed	0.0192	38	42.95	744.10

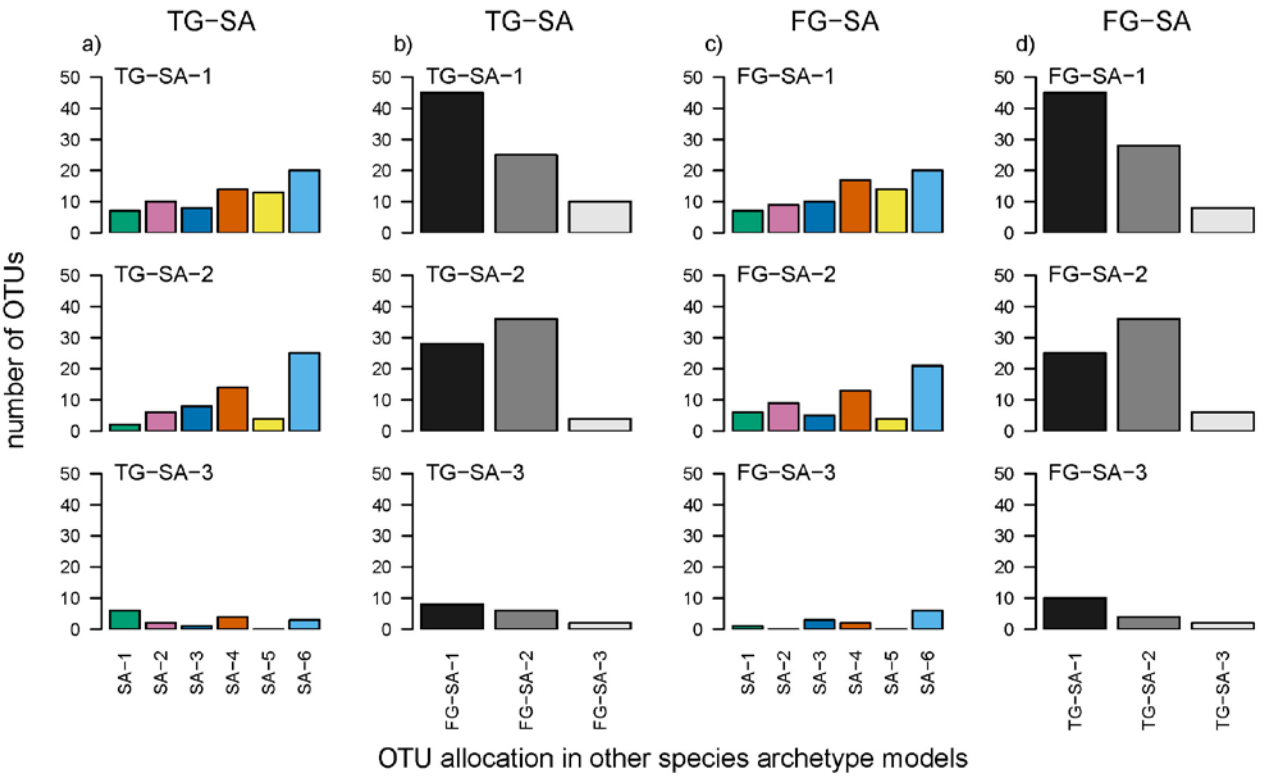
Appendix C

Supporting information for Chapter 4

Appendix C Figure 1: Likelihood of Akaike Information Criteria (aic) and Bayesian Information Criteria (bic) for the number of species archetypes for the OTU-dataset. The global maxima of the likelihood surface are estimated using 50 iterations of the same model with random starts, and extracting aic and bic values in each of those runs.



Appendix C Figure 2: Comparison between species archetype models using operational taxonomic units (OTUs) and the analysis using taxonomic (TG) and functional groups (FG). All panels show the number of OTUs within the respective species archetypes (SA), and colours indicate where these OTUs are located in either the high-resolution species archetypes **a**/**c**) or in the species archetypes based on grouped data **b**/**d**). Interestingly, although TG-SAs and FG-SAs share a similar number of OTUs from each of the high-resolution data SAs, around half of the species are not shared between each TG-SA and FG-SA.



Appendix C Table 1: Taxonomic classification of all operational taxonomic units (OTUs) identified from the camera images and the number of sites these OTUs were observed.

Annelida	# of sites
Perkinsiana sp.	25
Polychaeta sp. 2	12
Polychaeta sp. 3	8
unidentified empty tubes	5
Polychaeta sp. 6	4
Polychaeta sp. 5	4
Polynoidae sp.	3
Polychaeta sp. 4	3
Polychaeta sp. 1	3
Sabellidae sp.	2
Terebellidae sp.	1
unidentified Sedentaria sp.	1

Arthropoda	# of sites
Colossendeis sp.	9
unidentified Isopoda	6
unidentified species 3	4
Crustacea sp. 2	4
Chorismus antarcticus	4
Crustacea sp. 1	1

Brachiopoda	# of sites
Brachipoda sp.	1

Bryozoa	# of sites
unidentified Bryozoa	28
Cellarinelloides sp.	15
Pemmatoporella marginata	14
Bryozoa sp. 5	13
Cellarinelloides crassus	10
Bryozoa sp. 3	9
Camptoplites sp. 1	7
Camptoplites sp. 2	6
Bryozoa sp. 1	6
Cellarinella sp.	5
Bostrychopora dentata	4
Flustridae sp.	4
Bryozoa sp. 2	2
Reteporella gelida	2
Bryozoa sp. 4	1

Chordata	# of sites
Ascidia sp. 9	23
Ascidia sp. 5	17
unidentified Ascidia	17
Ascidia sp. 3	14
Ascidia sp. 4	12
Ascidia sp. 13	7
Ascidia sp. 6	3
Ascidia sp. 12	2
Ascidia sp. 8	2
Ascidia sp. 7	2
Ascidia sp. 2	2
Ascidia sp. 11	1
Ascidia sp. 10	1
Ascidia sp. 1	1

Cnidaria	# of sites
Thouarella sp.	24
Primnoidae sp. 3	21
unidentified Actinaria	21
Pennatulacea sp. 1	18
Actinaria sp. 2	16
Ceriantharia sp. 1	13
Primnoidae sp. 2	13
Hydrozoa sp. 1	12
unidentified Hydrozoa	12
Actinaria sp. 3	11
Anthozoa sp. 1	10
Stauromedusae sp.	10
Primnoidae sp. 1	10
Scleractinia sp.	8
Hydrozoa sp. 9	8
Hydrozoa sp. 7	8
Umbellula sp.	7
Anthomastus	6
Errina sp. 1	6
Hydrozoa sp. 8	5
Hydrozoa sp. 4	5
Actinaria sp. 1	5
Errina sp. 2	4
Zoantharia sp.	4
Hydrozoa sp. 2	4
unidentified Cnidaria	4
Primnoidae sp. 4	3
Actinaria sp. 4	3
Hydrozoa sp. 3	3
Pennatulacea cf.	2
Cerantharia sp. 2	2
Hydrozoa sp. 6	2
Hydrozoa sp. 10	1
Hydrozoa sp. 5	1

Ctenophora	# of sites
Lyrocteis flavopallidus	7

Echinodermata	# of sites
unidentified Ophiuroidae	33
Abatus sp.	31
Promachocrinus	29
unidentified Asteroidea	27
Synallactidae sp.	24
Dendrochirotida sp.	24
Notocidaris sp. 1	24
Astrotoma agassizii	22
unidentifiedHolothuroidae	21
Sterechinus sp.	18
Florometra mawsoni	16
Anthometrina adriani	13
Notocrinus virilis	11
unidentified Comatulidae	11
Diplasterias sp.	10
Psolidium sp.	10
Bathyplotes bongraini	8
Acodontaster conspicuus	7
Bathyplotes moseleyi	7
unidentified burying	
Ophiuridae	6
Echinodermata sp. 4	5
Holothuroidea sp. 1	5
Saliasterias sp.	4
Acodontaster capitatus	4
Holothuroidea sp. 3	4
Echinodermata sp. 5	3
Perknotaster sp.	2
Cuenotaster sp.	2
Holothuroidea sp. 2	2
Echinodermata sp. 3	1
Echinodermata sp. 2	1
Echinodermata sp. 1	1
Odontaster penicillatus	1
Psilaster charcoti	1
Remaster sp.	1
Lysasterias sp.	1
Holothuroidea sp. 4	1
Notocidaris sp. 2	1

Mollusca	# of sites
Mollusca sp. 4	14
Mollusca sp. 2	6
Mollusca sp. 5	4
Austrodoris kerguelensis	4
unidentified Mollusca	3
Mollusca sp. 7	2
Mollusca sp. 1	2
Mollusca sp. 8	1
Mollusca sp. 6	1
Mollusca sp. 3	1
Adamussium colbecki	1

Nemertea	# of sites
Nemertea sp.	8

Porifera	# of sites
unidentified Porifera	29
Antarctotetilla cf.	23
Rosalla cf. nuda	18
Cinachyra antarctica	15
Hemigellus cf.	15
Mycale acerata	14
Rosalla cf. villosa	12
Isodictya cf. toxophila	12
Rosella cf. fibulata	12
Guitarra cf. antarctica	11
Polymastia invaginata	11
Cinachyra/Craniella sp.	11
Haliclona sp. 1	10
Isodictya cf. lankesteri	10
Latrunculia cf. apicalis	9
Rosella cf.nuda	9
Stylocordyla	9
Tetillidae spp	7
Cinachyra/Craniella sp.	6
Calyx sp. 1	6
Inflatella belli	6
Clathria sp. 2	5
Kurikpatrickia variolosa	4
Haploscleriada spp.	4
Homaxinella cf.	4
Rossella cf. racovitzae	4
Dendrilla antarctica	3
Homaxinella cf.	3
Isodyctya sp. 1	3
Haliclona sp. 2	2
Mycale sp. 1	2
Haliclona cf. dancoi	2
Isodyctya erinacea	2
Tedania sp. 1	1
Sphaerotylus	1

Unidentified	# of sites
unidentified species 2	3
unidentified species 1	2
unidentified species 4	2
unidentified species 5	1

Appendix C Table 2: Number of OTUs within 30 categories of functional groups associated with each of the six species archetypes (SA-1 to SA-6). Functional groups are based on the traits of mobility, feeding-type and body-shape. Four OTUs with unknown functional traits are in the category 'unidentified'. The last column shows the number of OTUs not sorted into any species archetype. Feeding-types: DF = deposit feeder, Opp = opportunistic, PR = predator, aSF = active suspension feeders, pSF = passive suspension feeder

Mobility	Feeding	Body-shape	SA-1	SA-2	SA-3	SA-4	SA-5	SA-6	no SA
Mobile	DF	erect simple	1		1	1	2	2	
Mobile	DF	flat	1		2				
Mobile		erect simple	1			1		1	1
Mobile		flat				1		1	1
Mobile	Opp	erect simple					3		1
Mobile	Opp	flat	1				1		
Mobile	PR							1	
Mobile	PR	erect simple	1	2				2	
Mobile	PR	flat	1		2	2	1	11	4
Mobile	pSF	erect 3D branching					1		
Mobile	pSF	erect simple					1	2	
Sessile	aSF	ball-shaped		1	2	1	1		
Sessile	aSF	cuplike barrel		3					1
Sessile	aSF	cuplike tube		1		1		1	
Sessile	aSF	erect 2D laminar		1	2	2			
Sessile	aSF	erect 3D branching	1		1	1		1	1
Sessile	aSF	erect simple	2	4	1	2	1	4	1
Sessile	aSF	erect stalked	2			1	1	6	1
Sessile	aSF	massive						2	1
Sessile	DF	flat						1	
Sessile	PR	Anemone	1	2	1	2		2	1
Sessile	PR	erect stalked				1			
Sessile	pSF	Anemone	1	1		2		1	
Sessile	pSF	erect 2D fan-like						1	2
Sessile	pSF	erect 2D laminar				1		2	1
Sessile	pSF	erect 3D branching		2	4	8	4	6	2
Sessile	pSF	erect simple			1				
Sessile	pSF	erect stalked	1	1		3	1		3
Sessile	pSF	Tubeworm			1	2	1		
unidentified			2					1	1
TOTAL			**16**	**18**	**18**	**32**	**18**	**48**	**22**

Appendix C Table 3: Number of OTUs within 27 taxonomic groups associated with each of the six species archetypes (SA-1 to SA-6). Four OTUs are in the category 'unidentified' because they could not be sorted into one of the taxonomic groups. The last column shows the number of OTUs not sorted into any species archetype.

Taxonomic group	SA-1	SA-2	SA-3	SA-4	SA-5	SA-6	no SA
Annelidae	2		3	2	1	3	1
Ascidiacea	1	1		2	1	8	1
Asteroidae	1		2	2	1	8	2
Brachiopoda	1						
Bryozoa			1	5	1	5	3
Cnidaria - Hexacorallia	2	1	1	3		3	1
Cnidaria - Hydrozoa		1	2	3		4	1
Cnidaria - Octocorallia		1	1	2	3		2
Cnidaria - Staurozoa				1			
Crinoidae		2		2	1		
Crustacea	2	1				1	1
Ctenaria				1			
Echinidae					3		1
Holothuriae			1	2	3	4	
Mollusca	1	1				6	3
Nemertea				1			
Ophiuridae	1				2		
Porifera – Dendroceratida	1						
Porifera – Haplosclerida		1	1	1		2	
Porifera – Lyssacinosida		4					1
Porifera – Petrosina				1			
Porifera – Poecilosclerida	1	2	2	3		2	2
Porifera – Polymastida		1				1	
Porifera – Suberitida	1		1			1	
Porifera – Tetractinellida		1	2	1	1		
Pycnogonidae	1						
unidentified	1	1	1		1		3
TOTAL	**16**	**18**	**18**	**32**	**18**	**48**	**22**

Appendix C Table 4: Distribution of OTUs across the six archetypes. Shown are only those OTUs with a posterior probability greater than 0.8 of belonging to the respective archetypes.

SA-1	SA-3	SA-5	SA-6
Ascidia sp. 13	Acodontaster capitatus	Abatus sp.	Actinaria sp. 1
Austrodoris kerguelensis	Anthomastus bathyproctus	Antarctotetilla cf. grandis	Ascidia sp. 1
Brachipoda sp.	Bathyplotes moseleyi	Ascidia sp. 9	Ascidia sp. 2
Chorismus antarcticus	Bryozoa sp. 1	Astrotoma agassizii	Ascidia sp. 6
Colossendeis sp.	Cinachyra/Craniella sp. 2	Dendrochirotida sp.	Ascidia sp. 7
Dendrilla antarctica	Clathria sp. 2	Notocidaris sp. 1	Ascidia sp. 8
Echinodermata sp. 5	Errina sp. 1	Pennatulacea sp. 1	Ascidia sp. 10
Hydrozoa sp. 8	Errina sp. 2	Perkinsiana sp.	Ascidia sp. 11
Inflatella belli	Haploscleriada spp.	Primnoidae sp. 3	Ascidia sp. 12
Polychaeta sp. 6	Homaxinella cf. balfourensis	Promachocrinus kerguelensis	Bostrychopora dentata
Stylocordyla chupachups	Kurikpatrickia variolosa	Sterechinus sp.	Bryozoa sp. 2
unidentified burying Ophiuridae	Polychaeta sp. 5	Synallactidae sp.	Cellarinella sp.
unidentified empty tubes	Polynoidae sp.	Thouarella sp.	Cerantharia sp. 2
unidentified species 2	Sabellidae sp.	unidentified Asteroidea	Crustacea sp. 2
unidentified species 3	Saliasterias sp.	unidentified Bryozoa	Cuenotaster sp.
Zoantharia sp.	Scleractinia sp.	unidentified Holothuroidea	Echinodermata sp. 3
	Tetillidae spp	unidentified Ophiuoridea	Echinodermata sp. 4
	unidentified Cnidaria	unidentified Porifera	Flustridae sp.
SA-2	**SA-4**		Haliclona cf. dancoi
Actinaria sp. 3	Acodontaster conspicuus		Haliclona sp. 2
Anthometrina adriani	Actinaria sp. 2		Holothuroidea sp. 1
Cinachyra antarctica	Anthozoa sp. 1		Holothuroidea sp. 2
Haliclona sp. 1	Ascidia sp. 3		Holothuroidea sp. 3
Hydrozoa sp. 9	Ascidia sp. 4		Holothuroidea sp. 4
Isodictya cf. toxophila	Bathyplotes bongraini		Homaxinella cf. flagelliformis
Latrunculia cf. apicalis	Bryozoa sp. 3		Hydrozoa sp. 2
Mollusca sp. 4	Bryozoa sp. 5		Hydrozoa sp. 3
Polymastia invaginata	Calyx sp. 1		Hydrozoa sp. 4
Rosalla cf. nuda	Cellarinelloides crassus		Hydrozoa sp. 5
Rosalla cf. villosa	Cellarinelloides sp.		Hydrozoa sp. 10
Rosella cf. fibulata	Ceriantharia sp. 1		Isodyctya sp. 1
Rosella cf.nuda	Cinachyra/Craniella sp. 1		Lysasterias sp.
Umbellula sp.	Diplasterias sp.		Mollusca sp. 3
unidentified Actinaria	Florometra mawsoni		Mollusca sp. 5
unidentified Ascidia	Guitarra cf. antarctica		Mollusca sp. 6
unidentified Comatulidae	Hemigellus cf. fimbriatus		Mollusca sp. 7
unidentified Isopoda	Hydrozoa sp. 1		Mollusca sp. 8
	Hydrozoa sp. 7		Odontaster penicillatus
	Isodictya cf. lankesteri		Perknotaster sp.
	Lyrocteis flavopallidus		Polychaeta sp. 1
	Mycale acerata		Psilaster charcoti
	Nemertea sp.		Remaster sp.
	Notocrinus virilis		Reteporella gelida
	Pemmatoporella marginata		Sphaerotylus antarcticus
	Polychaeta sp. 2		Tedania sp. 1
	Polychaeta sp. 3		Terebellidae sp.
	Primnoidae sp. 1		unidentified Mollusca
	Primnoidae sp. 2		unidentified Sedentaria sp.
	Psolidium sp.		
	Stauromedusae sp.		
	unidentified Hydrozoa		

Appendix C Table 5: Table of mixing probabilities for those OTUs not clearly associated with one species archetype (i.e. where tau < 0.8). The highest probabilities are highlighted in bold.

	SA-1	SA-2	SA-3	SA-4	SA-5	SA-6
Actinaria sp. 4	0.001	0	**0.698**	0	0	0.3
Adamussium colbecki	0.232	0	0.195	0	0	**0.572**
Ascidia sp. 5	0	0	0	0.287	**0.713**	0
Bryozoa sp. 4	**0.67**	0	0.002	0	0	0.328
Camptoplites sp. 1	0	0	0	0.488	0	**0.512**
Camptoplites sp. 2	0.348	0	0	**0.64**	0	0.012
Crustacea sp. 1	0.216	0	0.003	0	0	**0.782**
Echinodermata sp. 1	0.005	0	0.311	0	0	**0.684**
Echinodermata sp. 2	**0.67**	0	0.002	0	0	0.328
Hydrozoa sp. 6	0.217	0	0	0.001	0	**0.782**
Isodyctya erinacea	0.003	0	**0.577**	0	0	0.42
Mollusca sp. 1	0.344	0	**0.518**	0	0	0.137
Mollusca sp. 2	0	0	0	**0.775**	0	0.225
Mycale sp. 1	0.2	0	0	0.001	0	**0.799**
Notocidaris sp. 2	0.005	0	0.311	0	0	**0.684**
Pennatulacea cf. Pennatula	0.174	0	**0.792**	0	0	0.033
Polychaeta sp. 4	**0.774**	0	0	0.001	0	0.226
Primnoidae sp. 4	0.333	0	**0.615**	0	0	0.052
Rossella cf. racovitzae	0.036	0	0.405	0.008	0	**0.55**
unidentified species 1	0.223	0	**0.392**	0	0	0.385
unidentified species 4	**0.656**	0	0.001	0	0	0.343
unidentified species 5	**0.67**	0	0.002	0	0	0.328

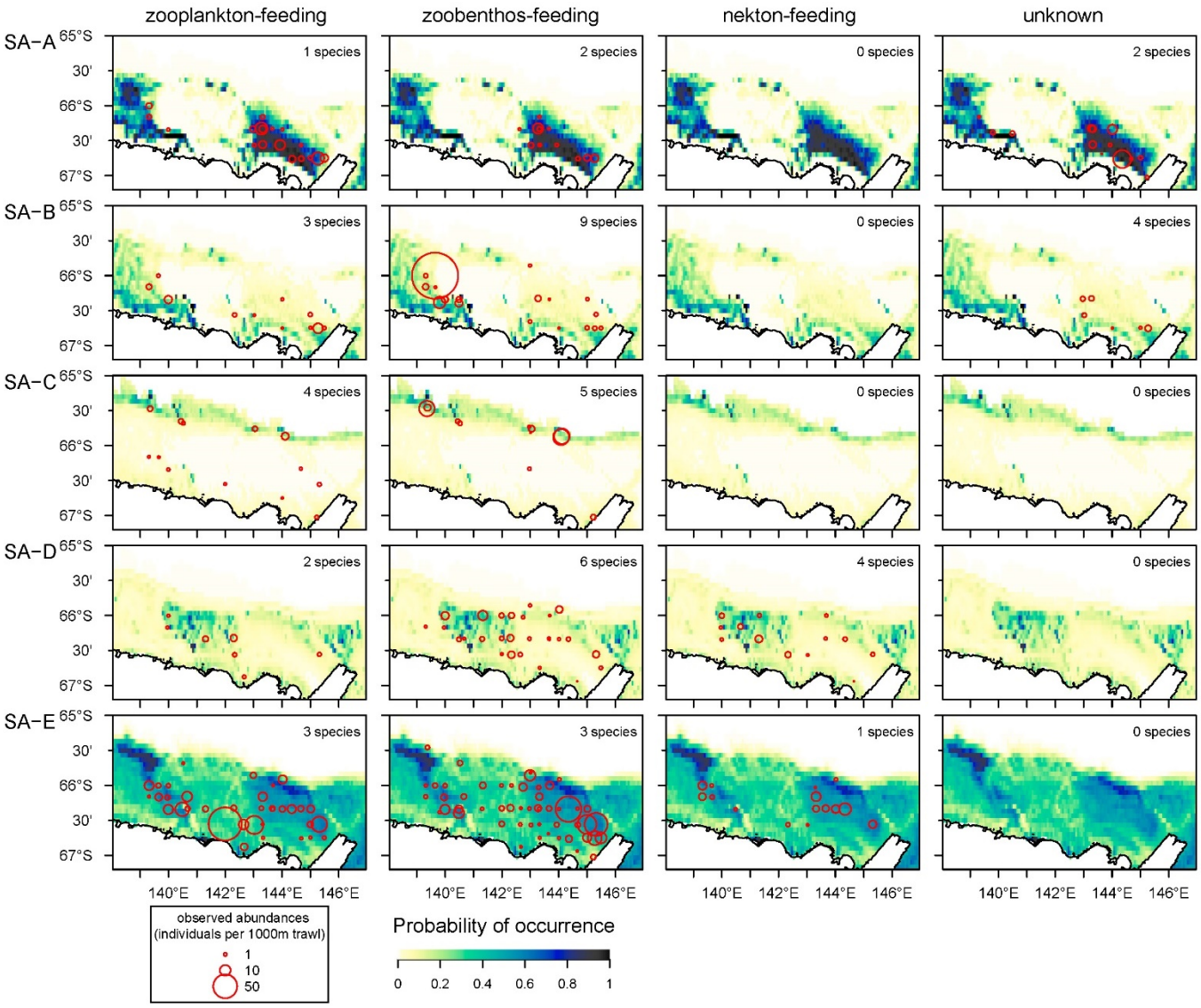
Appendix C Table 6: Coefficients (coef.) and standard error (se) for each of the six species archetype (SA-1 to SA-6). Coefficients larger than the standard error are highlighted in blue.

	Intercept	log(flux)	depth	depth^2	Seafloor tidal current speed	Settling particles	Slope of the seafloor	log(slope)	Seafloor current speed	Sinking particles	Topographic position index	temperature
coef.												
SA-1	-2.62	0.40	-1.85	-0.31	0.43	0.44	-0.89	0.76	-0.76	-0.11	0.81	0.31
SA-2	-1.20	0.39	-1.91	-2.05	0.23	0.36	-0.52	0.99	-0.39	-0.45	-0.42	1.19
SA-3	-8.22	1.51	5.11	0.96	-2.56	5.64	-2.83	11.73	0.51	-2.55	-2.47	-0.47
SA-4	-1.22	0.33	1.50	0.18	-0.44	0.27	0.84	-0.53	0.09	-0.33	-0.42	-0.58
SA-5	0.40	0.38	0.09	0.03	-0.08	0.60	-0.04	-0.21	0.23	-0.52	0.14	-0.02
SA-6	-3.56	0.05	3.79	2.02	-0.42	0.48	1.20	-0.65	0.49	-0.47	-0.41	-0.27
se												
SA-1	0.24	0.44	1.22	1.18	0.27	0.58	0.78	0.66	0.62	0.39	0.39	0.38
SA-2	0.12	0.26	0.62	0.69	0.21	0.38	0.51	0.45	0.31	0.26	0.26	0.30
SA-3	1.68	0.71	2.42	1.52	0.97	1.62	1.06	3.12	0.53	1.07	0.84	1.42
SA-4	0.10	0.16	0.48	0.59	0.12	0.17	0.35	0.21	0.21	0.16	0.20	0.21
SA-5	0.08	0.19	0.48	0.57	0.14	0.23	0.40	0.26	0.24	0.18	0.19	0.24
SA-6	0.26	0.24	1.13	1.05	0.23	0.24	0.62	0.29	0.37	0.26	0.42	0.44

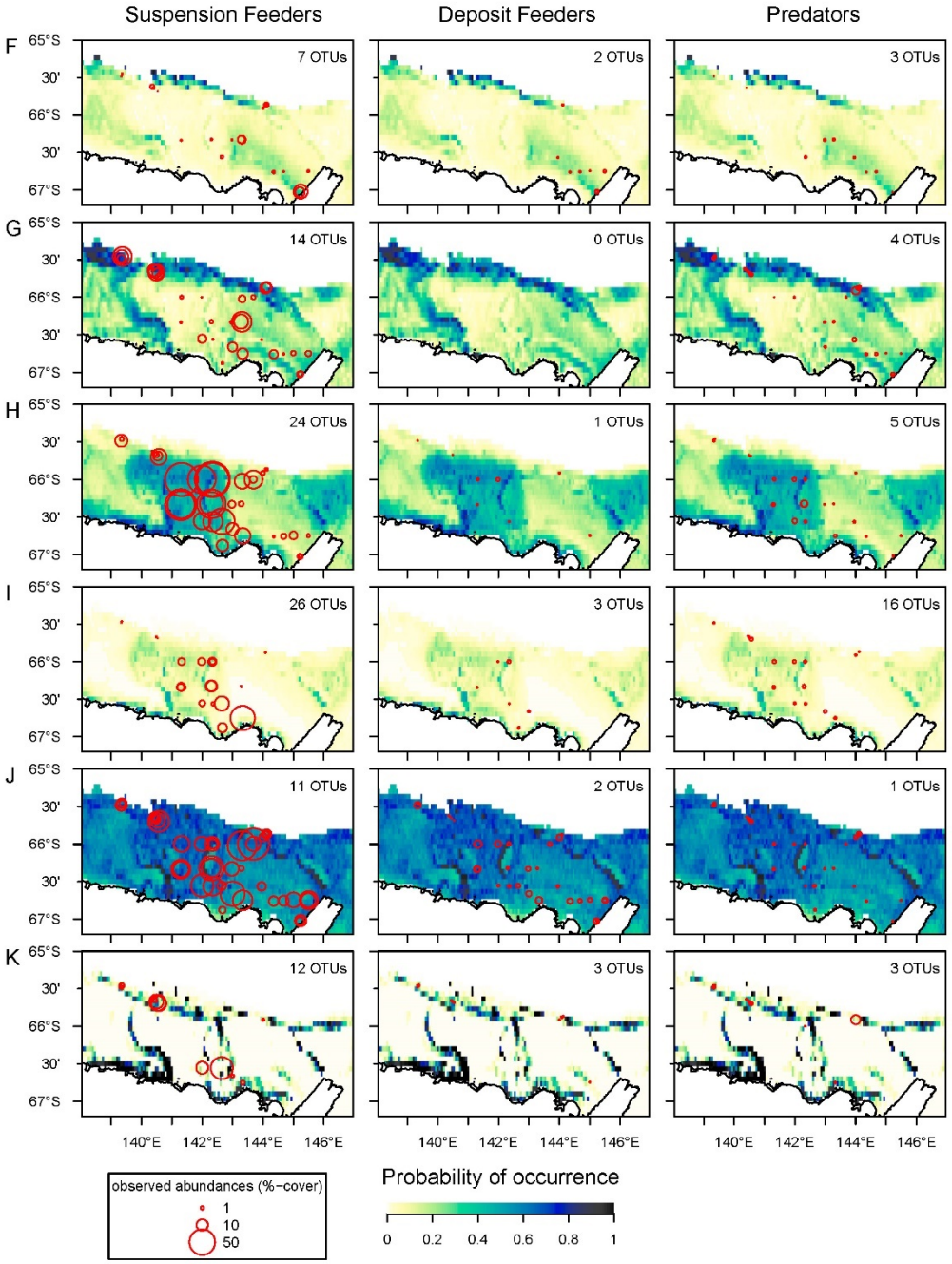
Appendix D

Supporting information for Chapter 5

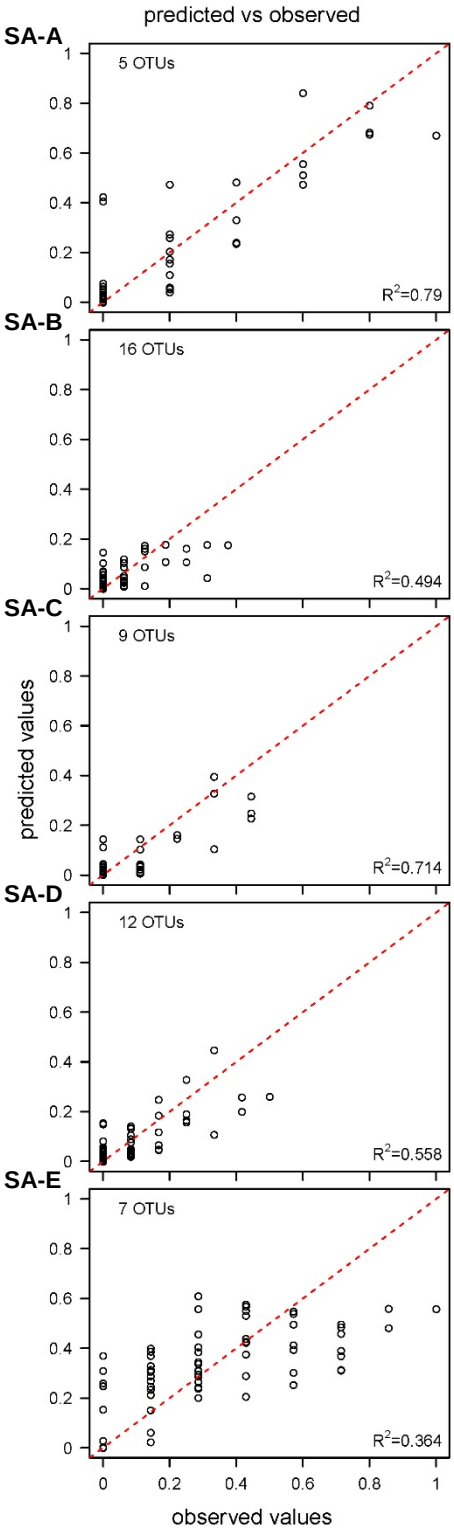
Appendix D Figure 1: Observed total counts of demersal fish per main feeding-type and species archetype. The underlying maps indicate the spatial distribution of the probability of occurrence for each species archetype. The big aggregation of zoobenthos-feeding fish in SA-B is a school of *Trematomus tokarevi*.



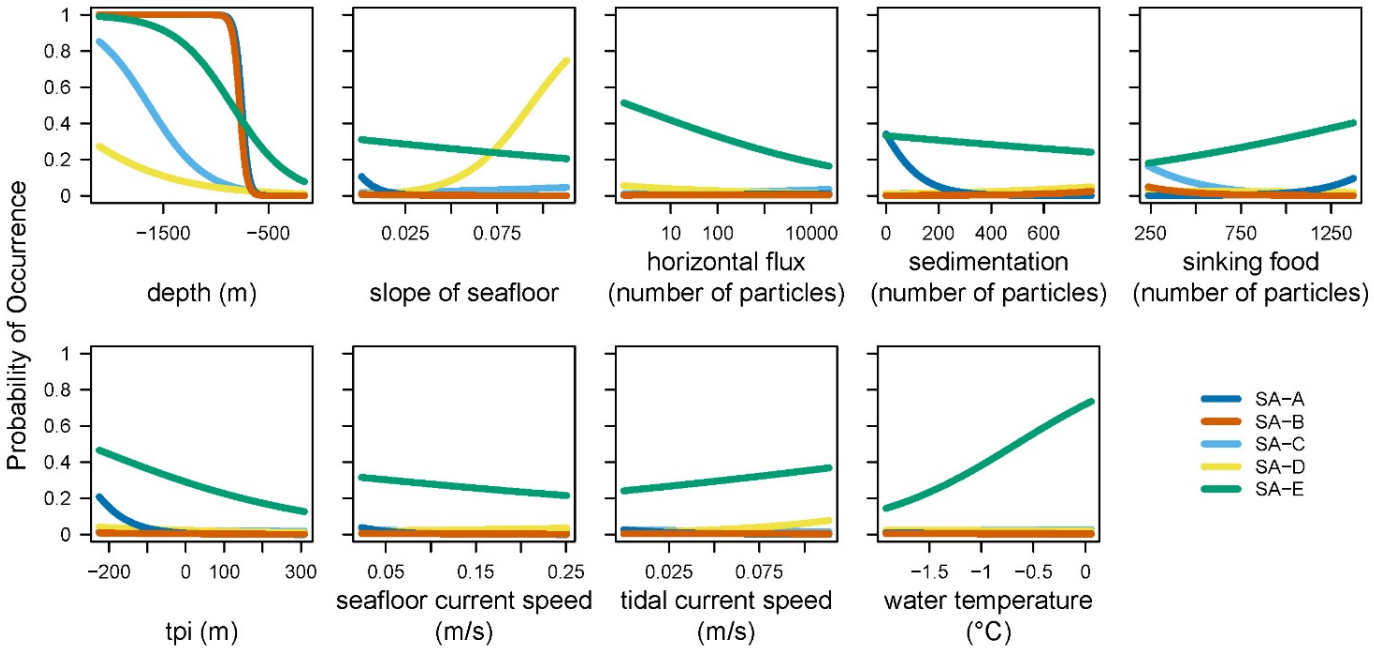
Appendix D Figure 2: Observed total abundances of benthic macro-invertebrates per main feeding-type and species archetype from Jansen et al. (2018b). The underlying maps indicate the spatial distribution of the probability of occurrence for each species archetype. OTUs= Operational taxonomic units (= species or other groups of morphologically resembling fauna identified to the highest possible taxonomic resolution). Letters **F-K** identify each species archetype and are identical to the letters used in Fig. 5.4.



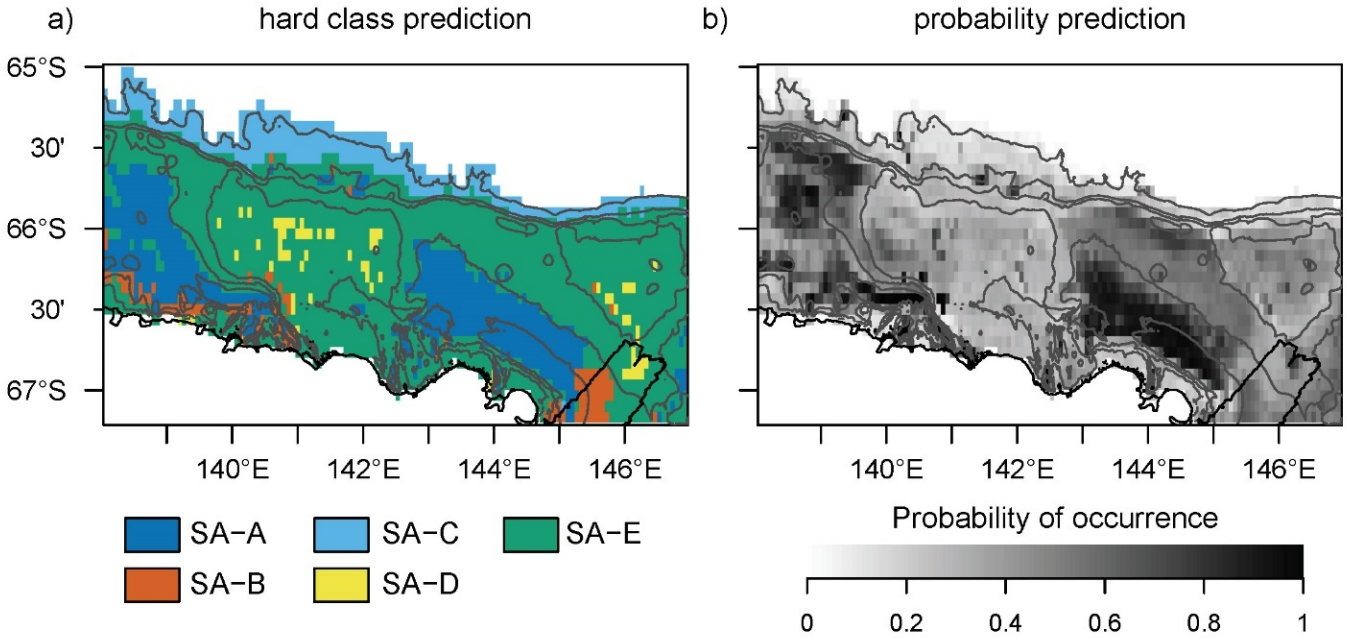
Appendix D Figure 3: Predicted values from the species archetype models versus observed values from the sample-sites (the probability of occurrence across all species in each species archetype). The red dotted line indicates the 1:1 line between predicted and observed values; the R^2-value is for a linear regression between observed and predicted values. The predictions are based on trawl-data from 68 sites. From top to bottom: **SA-A** (Species Archetype - A) to **SA-E**.



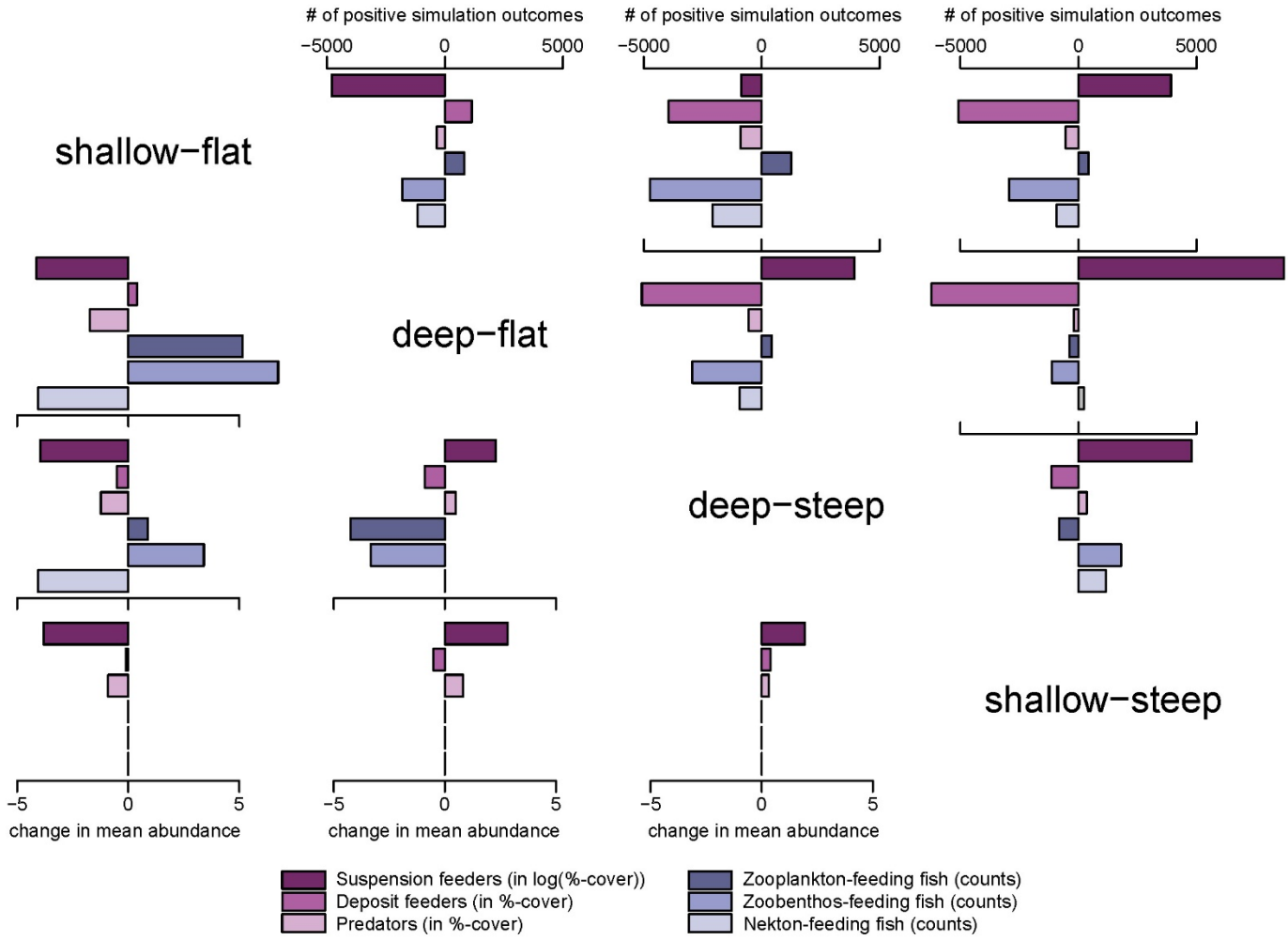
Appendix D Figure 4: Probability of occurrence for five species archetypes of demersal fish in relation to each of the environmental variables used in the analysis. Species archetypes change strongly along an environmental gradient if the line is steep, indicating which environmental predictor variables are important in determining high or low probability of occurrence for each species archetypes. tpi= topographic position index



Appendix D Figure 5: Hard classed distribution of five species archetype predictions for demersal fish across the George V shelf, East Antarctica. Map **(a)** identifies which assemblage of species is most likely to be encountered at any specific prediction point across the study area. **(b)** shows the probability of occurrence for the most likely archetype.



Appendix D Figure 6: Cross-comparison of changes in macro-invertebrate and fish functional groups between Antarctic benthic habitats. The top-right part of the figure shows the change between habitats for each functional group, as predicted from the qualitative network model (the difference in total positive outcomes after 10000 press-perturbations). The bottom-left shows the observed change in functional group abundance approximated through the species archetype models (see methods for details on the calculation). Note that the species archetype models suggest no distinct assemblage of demersal fish inhabits the shallow-steep environment, which is why data for demersal fish is missing from the three bottom panels.



Appendix D Table 1: Taxonomic family, species identity, feeding-type and associated species archetype (colour coded for easier interpretation) for each demersal fish-species used in this study. The last column identifies the source used to identify the feeding-type. Sub-families are identified for the Nototheniidae (Nototh.). * = feeding-type information from unpublished data.

Family	Species	Feeding-type	Species Archetype	Reference
Nototh. - Artedidraconidae	Artedidraco loennbergi	zoobenthos	SA-E (wide distr., medium depth)	www.fishbase.com
Nototh. - Artedidraconidae	Artedidraco shackletoni	zoobenthos	SA-D (banks)	www.fishbase.com
Nototh. - Artedidraconidae	Artedidraco skottsbergi	zoobenthos	SA-D (banks)	www.fishbase.com
Nototh. - Artedidraconidae	Dolloidraco longedorsalis	zoobenthos	SA-A (basins - common species)	www.fishbase.com
Nototh. - Artedidraconidae	Histiodraco velifer	zooplankton	SA-D (banks)	www.fishbase.com
Nototh. - Artedidraconidae	Pogonophryne phyllopogon	zoobenthos	SA-D (banks)	Lombarte et al. (2003)
Nototh. - Artedidraconidae	Pogonophryne maculatus	zoobenthos	SA-B (basins - rare species)	Lombarte et al. (2003)
Nototh. - Artedidraconidae	Pogonophryne sp.	zoobenthos	SA-B (basins - rare species)	Lombarte et al. (2003)
Nototh. - Bathydraconidae	Acanthodraco dewitti			
Nototh. - Bathydraconidae	Akarotaxis nudiceps		SA-A (basins - common species)	www.fishbase.com
Nototh. - Bathydraconidae	Bathydraco antarcticus		SA-B (basins - rare species)	
Nototh. - Bathydraconidae	Bathydraco macrolepis		SA-B (basins - rare species)	www.fishbase.com
Nototh. - Bathydraconidae	Bathydraco marri		SA-B (basins - rare species)	
Nototh. - Bathydraconidae	Cygnodraco mawsoni	nekton	SA-D (banks)	www.fishbase.com
Nototh. - Bathydraconidae	Gerlachea australis	zooplankton	SA-A (basins - common species)	www.fishbase.com
Nototh. - Bathydraconidae	Gymnodraco acuticeps	nekton	SA-D (banks)	www.fishbase.com
Nototh. - Bathydraconidae	Prionodraco evansii	zoobenthos	SA-D (banks)	www.fishbase.com
Nototh. - Bathydraconidae	Racovitzia glacialis	zooplankton	SA-E (wide distr., medium depth)	www.fishbase.com
Nototh. - Bathydraconidae	Vomeridens infuscipinnis		SA-A (basins - common species)	www.fishbase.com
Nototh. - Channichthyidae	Chaenodraco wilsoni	zooplankton	SA-B (basins - rare species)	www.fishbase.com
Nototh. - Channichthyidae	Chionobathyscus dewitti	zooplankton	SA-C (shelf-break)	www.fishbase.com
Nototh. - Channichthyidae	Chionodraco hamatus	nekton	SA-E (wide distr., medium depth)	www.fishbase.com
Nototh. - Channichthyidae	Chionodraco myersi	zooplankton	SA-B (basins - rare species)	www.fishbase.com
Nototh. - Channichthyidae	Cryodraco antarcticus	zooplankton	SA-E (wide distr., medium depth)	www.fishbase.com
Nototh. - Channichthyidae	Dacodraco hunteri		SA-B (basins - rare species)	www.fishbase.com
Nototh. - Channichthyidae	Neopagetopsis ionah	zooplankton	SA-C (shelf-break)	www.fishbase.com
Nototh. - Channichthyidae	Pagetopsis macropterus	nekton	SA-D (banks)	www.fishbase.com
Nototh. - Channichthyidae	Pagetopsis maculatus	nekton	SA-D (banks)	www.fishbase.com; *
Nototh. - Nototheniidae	Trematomus eulepidotus	zooplankton	SA-E (wide distr., medium depth)	www.fishbase.com
Nototh. - Nototheniidae	Trematomus hansoni	zooplankton		www.fishbase.com
Nototh. - Nototheniidae	Trematomus lepidorhinus/loennbergii	zoobenthos	SA-E (wide distr., medium depth)	
Nototh. - Nototheniidae	Trematomus newnesi	zooplankton	SA-B (basins - rare species)	www.fishbase.com
Nototh. - Nototheniidae	Trematomus pennellii	zoobenthos	SA-D (banks)	www.fishbase.com
Nototh. - Nototheniidae	Trematomus scotti	zooplankton	SA-E (wide distr., medium depth)	www.fishbase.com
Nototh. - Nototheniidae	Trematomus tokarevi	zoobenthos	SA-B (basins - rare species)	www.fishbase.com
Liparidae	Careproctus longipectoralis	zoobenthos	SA-C (shelf-break)	Duhamel et al. (2010)
Liparidae	Edentoliparis terraenovae	zooplankton	SA-B (basins - rare species)	Duhamel et al. (2010)
Liparidae	Paraliparis antarcticus	zoobenthos	SA-B (basins - rare species)	Duhamel et al. (2010)
Liparidae	Paraliparis charcoti	zoobenthos	SA-B (basins - rare species)	Duhamel et al. (2010)
Liparidae	Paraliparis leobergi	zoobenthos	SA-D (banks)	Duhamel et al. (2010)

Appendix D Table 1 continued: Taxonomic family, species identity, feeding-type and associated species archetype (colour coded for easier interpretation) for each demersal fish-species used in this study. The last column identifies the source used to identify the feeding-type.

Family	Species	Feeding-type	Species Archetype	Reference
Liparidae	Paraliparis mawsoni	zoobenthos	SA-C (shelf-break)	Duhamel et al. (2010)
Liparidae	Paraliparis valentinae	zoobenthos		Duhamel et al. (2010)
Macrouridae	Macrourus whitsoni	zoobenthos	SA-C (shelf-break)	www.fishbase.com
Muraenolepididae	Muraenolepis sp.	zooplankton	SA-C (shelf-break)	
Zoarcidae	Lycenchelys antarcticus	zoobenthos		Duhamel et al. (2010)
Zoarcidae	Lycenchelys aratrirostris	zoobenthos	SA-B (basins - rare species)	Duhamel et al. (2010)
Zoarcidae	Lycenchelys tristichodon	zoobenthos	SA-B (basins - rare species)	Duhamel et al. (2010)
Zoarcidae	Lycenchelys xanthoptera	zoobenthos	SA-C (shelf-break)	Duhamel et al. (2010)
Zoarcidae	Lycodapus pachysoma	zooplankton	SA-C (shelf-break)	Duhamel et al. (2010)
Zoarcidae	Lycodichthys antarcticus	zoobenthos	SA-D (banks)	Duhamel et al. (2010)
Zoarcidae	Oidiphorus mcallisteri	zoobenthos	SA-C (shelf-break)	Duhamel et al. (2010)
Zoarcidae	Ophthalmolycus amberensis	zoobenthos	SA-A (basins - common species)	Duhamel et al. (2010)
Zoarcidae	Pachycara brachycephalus	zoobenthos	SA-B (basins - rare species)	Duhamel et al. (2010)
Zoarcidae	Pachycara sp.	zoobenthos		Duhamel et al. (2010)

Appendix D Table 2: Notes and some relevant references for the signed interaction nodes in the qualitative network diagram. P=positive, N=negative, uncertain or weak links marked in grey.

From	To	sign	Notes	reference
Pelagic food sources	Surface-derived food near seafloor	P	High export ratios for primary production and particulate organic carbon in the Southern Ocean	Henson et al. (2012)
Depth of seafloor	Surface-derived food near seafloor	N	Decomposition of food-particles during sinking	
Depth of seafloor	Tidal-current speed	N	Same volume of water moving over shallow areas induces higher tidal-current speeds	
Slope of seafloor	Food-deposition / sedimentation	N	Particles less likely to settle on sloped surfaces	
Slope of seafloor	Hard substratum	P	Particles less likely to settle on sloped surfaces	
Ocean-current speed	Suspended food	P	Ocean-currents resuspend food-particles	Jansen et al. (2018c)
Ocean-current speed	Food-deposition / sedimentation	N	Ocean-currents resuspend food-particles	Jansen et al. (2018c)
Tidal-current speed	Suspended food	P	Ocean-currents resuspend food-particles	Jansen et al. (2018c)
Tidal-current speed	Food-deposition / sedimentation	N	Ocean-currents resuspend food-particles	Jansen et al. (2018c)
Surface-derived food near seafloor	Food-deposition / sedimentation	P	More particles -> more sedimentation	
Surface-derived food near seafloor	Suspended food	P	More particles -> more resuspension	
Food-deposition / sedimentation	Hard substratum	N	Hard substrata decrease with food-deposition, but uncertain how strong this link is relative to the strong link between hard substrata and slope	
Food-deposition / sedimentation	Mobile deposit feeders	P	Deposit feeders are more abundant where sedimentation is higher	Jansen et al. (2018c)
Food-deposition / sedimentation	Sessile suspension feeders	N	Strength of link uncertain. Deposition of food has been shown to influence suspension feeder abundance less than suspended food	Jansen et al. (2018c)
Suspended food	Sessile suspension feeders	P	Suspension feeders are more abundant where suspended food is abundant	Jansen et al. (2018c)
Hard substratum	Mobile deposit feeders	N	Deposit feeders prefer soft substrata	
Hard substratum	Sessile suspension feeders	P	Suspension feeders need hard substrata for attachment	
Mobile deposit feeders	Zoobenthos feeding fish	P / N	Predator-prey interaction	
Mobile deposit feeders	Mobile predators	P / N	Predator-prey interaction	
Sessile suspension feeders	Mobile predators	P	Provide habitat, but strength of link uncertain	
Sessile suspension feeders	Zoobenthos feeding fish	P	Provide habitat, but strength of link uncertain	
Mobile predators	Zoobenthos feeding fish	P / N	Predator-prey interaction	
Pelagic food sources	Zooplankton feeding fish	P	Predator-prey interaction, but size of the negative effect of zooplankton feeding fish on zooplankton unknown, and therefore not included here	
Zoobenthos feeding fish	Nekton feeding fish	P / N	Predator-prey interaction, but role of each prey source and the strength of link uncertain	
Zooplankton feeding fish	Nekton feeding fish	P / N	Predator-prey interaction, but role of each prey source and the strength of link uncertain	

Appendix D Table 3: Setup of press-perturbations of the dynamic network model. Using QPress, both depth and slope are given either positive (+) or negative (-) press-perturbations for simulating changes in the ecosystem between the four main habitats.

Press-perturbation		Change in ecosystem characteristics	Main occurrence of the habitat
Depth	Slope		
+	+	Deeper & steeper	Shelf-break and slope
+	-	Deeper & more level	Shelf-depressions and Sills
-	+	Shallower & steeper	Edges of the banks and along the coastline
-	-	Shallower & more level	Top of the banks

Appendix D Table 4: Abundances of different feeding types of demersal fish and benthic macro-invertebrates in each species archetype (SA-A to SA-E, and SA-1 to SA-6). Values are calculated in two steps: First, the mean abundance of each species is calculated for all sites where this species is present. Second, the average abundances of every species with both the same feeding-type and the same species archetype are summed up. For demersal fish, abundance is given as number of individuals caught on average, while for benthic macro-invertebrate the abundance is given as average %-cover. In SA-B, a large school of *Trematomus tokarevi* contributed to the high value for the benthos-feeding fish (the amount of benthos-feeding fish other than *T. tokarevi* is 10.46). Comic-icons above the table indicate the main habitat corresponding to each pair of species archetypes. From left to right, these are: Deep-flat, deep-steep, shallow-flat, widely distributed, shallow-steep.

fish	**SA-A**	**SA-B**	**SA-C**	**SA-D**		**SA-E**	
Plankton feeder	4.00	4.77	4.51	3.63		13.28	
Benthos feeder	3.34	50.31	12.28	8.87		10.46	
Nekton feeder				4.05		3.74	
invertebrates	**SA-1**		**SA-2**	**SA-4**	**SA-6**	**SA-5**	**SA-3**
Suspension feeder	5.78		15.65	63.18	72.00	27.39	22.59
Deposit feeder	0.91			0.29	0.72	1.91	0.39
Predator	0.52		1.01	1.53	2.95	0.45	1.34

Appendix D Table 5: Mean values for the pearson correlation between predicted species archetype distributions of demersal fish and benthic macro-invertebrates. Higher values indicate stronger correlations between the distributions of the assemblages.

	SA-F	**SA-G**	**SA-H**	**SA-I**	**SA-J**	**SA-K**
SA-A	0.055	-0.024	-0.217	-0.432	-0.373	-0.076
SA-B	0.245	0.491	-0.015	-0.132	0.043	0.309
SA-C	0.158	0.491	0.035	0.039	0.171	0.269
SA-D	-0.355	-0.285	0.353	0.436	0.212	-0.166
SA-E	-0.211	-0.076	-0.164	-0.108	-0.22	-0.244

Bibliography

AAD. 2017. Australian Antarctic Division: A Proposal for a Marine Protected Area in the East Antarctic Planning Domain. www.antarctica.gov.au/law-and-treaty/ccamlr/marine-protected-areas. Accessed: 01.12.2017

Althaus, F., N. Hill, R. Ferrari, L. Edwards, R. Przeslawski, C. H. Schönberg, R. Stuart-Smith, N. Barrett, G. Edgar, and J. Colquhoun. 2015. A Standardised Vocabulary for Identifying Benthic Biota and Substrata from Underwater Imagery: The Catami Classification Scheme. *PLoS One* **10**:e0141039.

Anderson, O. F., J. M. Guinotte, A. A. Rowden, M. R. Clark, S. Mormede, A. J. Davies, and D. A. Bowden. 2016. Field Validation of Habitat Suitability Models for Vulnerable Marine Ecosystems in the South Pacific Ocean: Implications for the Use of Broad-Scale Models in Fisheries Management. *Ocean & Coastal Management* **120**:110-126.

Angel, M. V. 1993. Biodiversity of the Pelagic Ocean. *Conservation Biology* **7**:760-772.

Anthony, K. R. N., J. M. Dambacher, T. Walshe, and R. Beeden. 2013. A Framework for Understanding Cumulative Impacts, Supporting Environmental Decisions and Informing Resilience Based Management of the Great Barrier Reef World Heritage Area. Report to the Australian Government Department of the Environment.

Aoki, S., R. Kobayashi, S. Rintoul, T. Tamura, and K. Kusahara. 2017. Changes in Water Properties and Flow Regime on the Continental Shelf Off the Adélie/George V Land Coast, East Antarctica, after Glacier Tongue Calving. *Journal of Geophysical Research: Oceans* **122**:6277–6294.

Armand, L. K., X. Crosta, O. Romero, and J.-J. Pichon. 2005. The Biogeography of Major Diatom Taxa in Southern Ocean Sediments: 1. Sea Ice Related Species. *Palaeogeography, Palaeoclimatology, Palaeoecology* **223**:93-126.

Armand, L. K., and U. Zielinski. 2001. Diatom Species of the Genus Rhizosolenia from Southern Ocean Sediments: Distribution and Taxonomic Notes. *Diatom research* **16**:259-294.

Arrigo, K. R., and G. L. van Dijken. 2003. Phytoplankton Dynamics within 37 Antarctic Coastal Polynya Systems. *Journal of Geophysical Research: Oceans* **108**.

Arrigo, K. R., G. L. van Dijken, D. G. Ainley, M. A. Fahnestock, and T. Markus. 2002. Ecological Impact of a Large Antarctic Iceberg. *Geophysical Research Letters* **29**:8-1-8-4.

Arrigo, K. R., G. L. van Dijken, and A. L. Strong. 2015. Environmental Controls of Marine Productivity Hot Spots around Antarctica. *Journal of Geophysical Research: Oceans* **120**:5545-5565.

Baddeley, A., and R. Turner. 2005. Spatstat: An R Package for Analyzing Spatial Point Patterns. *Journal of Statistical Software* **12**:1-42.

Barber, D., and R. Massom. 2007. A Bi-Polar Assessment of Modes of Polynya Formation. Pages 1-54 *in* W. O. Smith and D. G. Barber, (eds). Polynyas: Windows to the World's Oceans. Elsevier, Amsterdam.

Barnes, D. K. A. 2017. Polar Zoobenthos Blue Carbon Storage Increases with Sea Ice Losses, Because across-Shelf Growth Gains from Longer Algal Blooms Outweigh Ice Scour Mortality in the Shallows. *Global Change Biology* **23**:5083-5091.

Barnes, D. K. A., and C. J. Sands. 2017. Functional Group Diversity Is Key to Southern Ocean Benthic Carbon Pathways. *PLoS One* **12**:e0179735.

Barrett, N. S., J. Sanderson, M. Lawler, V. Halley, and A. Jordan. 2001. Mapping of Inshore Marine Habitats in South-Eastern Tasmania for Marine Protected Area Planning and Marine Management.

Barry, J. P., and P. K. Dayton. 1988. Current Patterns in Mcmurdo Sound, Antarctica and Their Relationship to Local Biotic Communities. *Polar Biology* **8**:367-376.

Barry, J. P., J. M. Grebmeier, J. Smith, and R. B. Dunbar. 2003. Oceanographic Versus Seafloor-Habitat Control of Benthic Megafaunal Communities in the S.W. Ross Sea, Antarctica. Pages 327-353 *in* G. R. Ditullio and R. B. Dunbar, (eds). Biogeochemistry of the Ross Sea. American Geophysical Union, Washington, D. C.

Bax, N. J. 2011. Marine Biodiversity Hub, Commonwealth Environment Research Facilities, Final Report 2007-2010. Report to Department of Sustainability, Environment and Communities. Canberra, Australia.

Beaman, R. J., and P. T. Harris. 2003. Seafloor Morphology and Acoustic Facies of the George V Land Shelf. *Deep-Sea Research Part II: Topical Studies in Oceanography* **50**:1343-1355.

Beaman, R. J., and P. T. Harris. 2005. Bioregionalization of the George V Shelf, East Antarctica. *Continental Shelf Research* **25**:1657-1691.

Beaman, R. J., P. E. O'Brien, A. L. Post, and L. De Santis. 2011. A New High-Resolution Bathymetry Model for the Terre Adelie and George V Continental Margin, East Antarctica. *Antarctic Science* **23**:95-103.

Beans, C., J. H. Hecq, P. Koubbi, C. Vallet, S. Wright, and A. Goffart. 2008. A Study of the Diatom-Dominated Microplankton Summer Assemblages in Coastal Waters from Terre Adélie to the Mertz Glacier, East Antarctica (139°E–145°E). *Polar Biology* **31**:1101-1117.

Beazley, L., E. Kenchington, I. Yashayaev, and F. J. Murillo. 2015. Drivers of Epibenthic Megafaunal Composition in the Sponge Grounds of the Sackville Spur, Northwest Atlantic. *Deep-Sea Research Part I: Oceanographic Research Papers* **98**:102-114.

Beger, M., and H. P. Possingham. 2008. Environmental Factors That Influence the Distribution of Coral Reef Fishes: Modeling Occurrence Data for Broad-Scale Conservation and Management. *Marine Ecology Progress Series* **361**:1-13.

Bergkemper, V., and T. Weisse. 2018. Do Current European Lake Monitoring Programmes Reliably Estimate Phytoplankton Community Changes? *Hydrobiologia* **824**:143-162.

Bevilacqua, S., A. Terlizzi, J. Claudet, S. Fraschetti, and F. Boero. 2012. Taxonomic Relatedness Does Not Matter for Species Surrogacy in the Assessment of Community Responses to Environmental Drivers. *Journal of Applied Ecology* **49**:357-366.

Blanchard, J. L., R. F. Heneghan, J. D. Everett, R. Trebilco, and A. J. Richardson. 2017. From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. *Trends in Ecology and Evolution* **32**:174-186.

Blondeau-Patissier, D., J. F. Gower, A. G. Dekker, S. R. Phinn, and V. E. Brando. 2014. A Review of Ocean Color Remote Sensing Methods and Statistical Techniques for the Detection, Mapping and Analysis of Phytoplankton Blooms in Coastal and Open Oceans. *Progress in Oceanography* **123**:123-144.

Boakes, E. H., P. J. McGowan, R. A. Fuller, D. Chang-qing, N. E. Clark, K. O'Connor, and G. M. Mace. 2010. Distorted Views of Biodiversity: Spatial and Temporal Bias in Species Occurrence Data. *PLoS Biology* **8**:e1000385.

Brandt, A., C. De Broyer, I. De Mesel, K. E. Ellingsen, A. J. Gooday, B. Hilbig, K. Linse, M. R. A. Thomson, and P. A. Tyler. 2007. The Biodiversity of the Deep Southern Ocean Benthos. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**:39-66.

Brasier, M. J., J. Harle, H. Wiklund, R. M. Jeffreys, K. Linse, H. A. Ruhl, and A. G. Glover. 2017. Distributional Patterns of Polychaetes across the West Antarctic Based on DNA Barcoding and Particle Tracking Analyses. *Frontiers in Marine Science* **4**:356.

Bray, J. R., and J. T. Curtis. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs* **27**:325-349.

Brower, A. A., M. C. Ferguson, S. V. Schonberg, S. C. Jewett, and J. T. Clarke. 2017. Gray Whale Distribution Relative to Benthic Invertebrate Biomass and Abundance: Northeastern Chukchi Sea 2009–2012. *Deep Sea Research Part II: Topical Studies in Oceanography* **144**:156-174.

Brown, A. M., D. I. Warton, N. R. Andrew, M. Binns, G. Cassis, and H. Gibb. 2014. The Fourth-Corner Solution–Using Predictive Models to Understand How Species Traits Interact with the Environment. *Methods in Ecology and Evolution* **5**:344-352.

Brown, P. E. 2015. Model-Based Geostatistics the Easy Way. *Journal of Statistical Software* **63**:1-24.

Caburlotto, A., L. De Santis, C. Zanolla, A. Camerlenghi, and J. Dix. 2006. New Insights into Quaternary Glacial Dynamic Changes on the George V Land Continental Margin (East Antarctica). *Quaternary Science Reviews* **25**:3029-3049.

Cadotte, M. W., C. A. Arnillas, S. W. Livingstone, and S.-L. E. Yasui. 2015. Predicting Communities from Functional Traits. *Trends in Ecology & Evolution* **30**:510-511.

Campagne, P., X. Crosta, M. N. Houssais, D. Swingedouw, S. Schmidt, A. Martin, E. Devred, S. Capo, V. Marieu, I. Closset, and G. Masse. 2015. Glacial Ice and Atmospheric Forcing on the Mertz Glacier Polynya over the Past 250 Years. *Nature Communications* **6**:6642.

Canals, M., P. Puig, X. D. de Madron, S. Heussner, A. Palanques, and J. Fabres. 2006. Flushing Submarine Canyons. *Nature* **444**:354-357.

Cape, M. R., M. Vernet, M. Kahru, and G. Spreen. 2014. Polynya Dynamics Drive Primary Production in the Larsen a and B Embayments Following Ice Shelf Collapse. *Journal of Geophysical Research: Oceans* **119**:572-594.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity Loss and Its Impact on Humanity. *Nature* **486**:59-67.

Causse, R., C. Ozouf-Costaz, P. Koubbi, D. Lamy, M. Eléaume, A. Dettaï, G. Duhamel, F. Busson, P. Pruvost, A. Post, R. J. Beaman, and M. J. Riddle. 2011. Demersal Ichthyofaunal Shelf Communities from the Dumont D'urville Sea (East Antarctica). *Polar Science* **5**:272-285.

Cavalieri, D., C. Parkinson, P. Gloersen, and H. J. Zwally. 1996 , updated yearly. Sea Ice Concentrations from Nimbus-7 Smmr and Dmsp Ssm/I-Ssmis Passive Microwave Data, Version 1. *NASA DAAC at the National Snow and Ice Data Center, Boulder, Colorado USA*. http://doi.org/10.5067/8GQ8LZQVL0VL

CCAMLR. 2011. Convention for the Conservation of Antarctic Marine Living Resources (Ccamlr): Conservation Measure 91-04: General Framework for the Establishment of Ccamlr Marine Protected Areas. Available At: Www.Ccamlr.Org/Node/74905. Last Accessed 29th May 2018.

CCAMLR. 2018. Convention for the Conservation of Antarctic Marine Living Resources (Ccamlr): Convention Text. http://www.ccamlr.org/en/organisation/camlr-convention-text. Accessed: 01.10.2018

Champion, C., A. J. Hobday, S. R. Tracey, and G. T. Pecl. 2018. Rapid Shifts in Distribution and High-Latitude Persistence of Oceanographic Habitat Revealed Using Citizen Science Data from a Climate Change Hotspot. *Global Change Biology* **24**:5440-5453.

Chapin Iii, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, and S. E. Hobbie. 2000. Consequences of Changing Biodiversity. *Nature* **405**:234.

Chaudhary, C., H. Saeedi, and M. J. Costello. 2016. Bimodality of Latitudinal Gradients in Marine Species Richness. *Trends in Ecology & Evolution* **31**:670-676.

Choudhury, M., and A. Brandt. 2007. Composition and Distribution of Benthic Isopod (Crustacea, Malacostraca) Families Off the Victoria-Land Coast (Ross Sea, Antarctica). *Polar Biology* **30**:1431-1437.

Chown, S. L., A. Clarke, C. I. Fraser, S. C. Cary, K. L. Moon, and M. A. McGeoch. 2015. The Changing Form of Antarctic Biodiversity. *Nature* **522**:431-438.

Clark, G. F., E. M. Marzinelli, C. J. Fogwill, C. S. M. Turney, and E. L. Johnston. 2015. Effects of Sea-Ice Cover on Marine Benthic Communities: A Natural Experiment in Commonwealth Bay, East Antarctica. *Polar Biology* **38**:1213-1222.

Clarke, A., R. B. Aronson, J. A. Crame, J. M. Gil, and D. B. Blake. 2004. Evolution and Diversity of the Benthic Fauna of the Southern Ocean Continental Shelf. *Antarctic Science* **16**:559-568.

Clarke, A., H. J. Griffiths, D. K. A. Barnes, M. P. Meredith, and S. M. Grant. 2009. Spatial Variation in Seabed Temperatures in the Southern Ocean: Implications for Benthic Ecology and Biogeography. *Journal of Geophysical REsearch* **114**.

Constable, A. J., J. Melbourne‐Thomas, S. P. Corney, K. R. Arrigo, C. Barbraud, D. K. Barnes, N. L. Bindoff, P. W. Boyd, A. Brandt, and D. P. Costa. 2014. Climate Change and Southern Ocean Ecosystems I: How Changes in Physical Habitats Directly Affect Marine Biota. *Global Change Biology* **20**:3004-3025.

Convey, P., S. L. Chown, A. Clarke, D. K. A. Barnes, S. Bokhorst, V. Cummings, H. W. Ducklow, F. Frati, T. G. A. Green, S. Gordon, H. J. Griffiths, C. Howard-Williams, A. H. L. Huiskes, J. Laybourn-Parry, W. B. Lyons, A. McMinn, S. A. Morley, L. S. Peck, A. Quesada, S. A. Robinson, S. Schiaparelli, and D. H. Wall. 2014. The Spatial Structure of Antarctic Biodiversity. *Ecological Monographs* **84**:203-244.

Cougnon, E. A., B. K. Galton-Fenzi, A. J. S. Meijers, and B. Legresy. 2013. Modeling Interannual Dense Shelf Water Export in the Region of the Mertz Glacier Tongue (1992-2007). *Journal of Geophysical Research: Oceans* **118**:5858-5872.

Cougnon, E. A., B. K. Galton-Fenzi, S. R. Rintoul, B. Legrésy, G. D. Williams, A. D. Fraser, and J. R. Hunter. 2017. Regional Changes in Icescape Impact Shelf Circulation and Basal Melting. *Geophysical Research Letters* **44**:11519-11527.

Crosta, X., J. Crespin, I. Billy, and O. Ther. 2005. Major Factors Controlling Holocene Δ13corgchanges in a Seasonal Sea-Ice Environment, Adélie Land, East Antarctica. *Global Biogeochemical Cycles* **19**.

Crosta, X., M. Debret, D. Denis, M. A. Courty, and O. Ther. 2007. Holocene Long- and Short-Term Climate Changes Off Adélie Land, East Antarctica. *Geochemistry, Geophysics, Geosystems* **8**.

Cummings, V. J., S. F. Thrush, M. Chiantore, J. E. Hewitt, and R. Cattaneo-Vietti. 2010. Macrobenthic Communities of the North-Western Ross Sea Shelf: Links to Depth, Sediment Characteristics and Latitude. *Antarctic Science* **22**:793-804.

Cunningham, R. B., and D. B. Lindenmayer. 2005. Modeling Count Data of Rare Species: Some Statistical Issues. *Ecology* **86**:1135-1142.

D'Amen, M., C. Rahbek, N. E. Zimmermann, and A. Guisan. 2017. Spatial Predictions at the Community Level: From Current Approaches to Future Frameworks. *Biological Reviews of the Cambridge Philosophical Society* **92**:169-187.

Dambacher, J. M., D. J. Gaughan, M.-J. Rochet, P. A. Rossignol, and V. M. Trenkel. 2009. Qualitative Modelling and Indicators of Exploited Ecosystems. *Fish and Fisheries* **10**:305-322.

Dambacher, J. M., P. C. Rothlisberg, and N. R. Loneragan. 2015. Qualitative Mathematical Models to Support Ecosystem‐Based Management of Australia's Northern Prawn Fishery. *Ecological Applications* **25**:278-298.

Danovaro, R., C. Corinaldesi, G. D'Onghia, B. Galil, C. Gambi, A. J. Gooday, N. Lampadariou, G. M. Luna, C. Morigi, and K. Olu. 2010. Deep-Sea Biodiversity in the Mediterranean Sea: The Known, the Unknown, and the Unknowable. *PLoS One* **5**:e11832.

Dayton, P. K., and J. S. Oliver. 1977. Antarctic Soft-Bottom Benthos in Oligotrophic and Eutrophic Environments. *Science* **197**:55-58.

De Broyer, C., P. Koubbi, H. J. Griffiths, B. Raymond, C. d. Udekem d'Acoz, A. P. Van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Huettmann, A. Post, and Y. Ropert-Coudert. 2014. Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge.

De Vos, J. M., L. N. Joppa, J. L. Gittleman, P. R. Stephens, and S. L. Pimm. 2015. Estimating the Normal Background Rate of Species Extinction. *Conservation Biology* **29**:452-462.

Denis, D., X. Crosta, S. Schmidt, D. S. Carson, R. S. Ganeshram, H. Renssen, J. Crespin, O. Ther, I. Billy, and J. Giraudeau. 2009. Holocene Productivity Changes Off Adélie Land (East Antarctica). *Paleoceanography* **24**.

Dickey-Collas, M., M. R. Payne, V. M. Trenkel, and R. D. Nash. 2014. Hazard Warning: Model Misuse Ahead. *ICES Journal of Marine Science* **71**:2300-2306.

Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics* **41**:149-172.

Domack, E., and J. Anderson. 1983. Marine Geology of the George V Continental Margin: Combined Results of Deep Freeze 79 and the 1911-14 Australasian Expedition. Cambridge University Press, New York.

Dormann, C. F., J. M. McPherson, M. B. Araújo, R. Bivand, J. Bolliger, G. Carl, R. G. Davies, A. Hirzel, W. Jetz, and W. D. Kissling. 2007. Methods to Account for Spatial Autocorrelation in the Analysis of Species Distributional Data: A Review. *Ecography* **30**:609-628.

Douglass, L. L., J. Turner, H. S. Grantham, S. Kaiser, A. Constable, R. Nicoll, B. Raymond, A. Post, A. Brandt, and D. Beaver. 2014. A Hierarchical Classification of Benthic Biodiversity and Assessment of Protected Areas in the Southern Ocean. *PLoS One* **9**:e100551.

Duhamel, G., M. Hautecoeur, A. Dettai, R. Causse, P. Pruvost, F. Busson, A. Couloux, P. Koubbi, R. Williams, C. Ozouf-Costaz, and G. Nowara. 2010. Liparids from the Eastern Sector of Southern Ocean and First Information from Molecular Studies. *Cybium* **34**:319-343.

Duineveld, G., M. Lavaleye, and E. Berghuis. 2004. Particle Flux and Food Supply to a Seamount Cold-Water Coral Community (Galicia Bank, Nw Spain). *Marine Ecology Progress Series* **277**:13-23.

Dunstan, P. K., N. J. Bax, S. D. Foster, A. Williams, and F. Althaus. 2012. Identifying Hotspots for Biodiversity Management Using Rank Abundance Distributions. *Diversity and Distributions* **18**:22-32.

Dunstan, P. K., and S. D. Foster. 2011. Rad Biodiversity: Prediction of Rank Abundance Distributions from Deep Water Benthic Assemblages. *Ecography* **34**:798-806.

Dunstan, P. K., S. D. Foster, and R. Darnell. 2011. Model Based Grouping of Species across Environmental Gradients. *Ecological Modelling* **222**:955-963.

Dunstan, P. K., S. D. Foster, F. K. C. Hui, and D. I. Warton. 2013. Finite Mixture of Regression Modeling for High-Dimensional Count and Biomass Data in Ecology. *Journal of Agricultural Biological and Environmental Statistics* **18**:357-375.

Dutkiewicz, A., R. D. Muller, S. O'Callaghan, and H. Jonasson. 2015. Census of Seafloor Sediments in the World's Ocean. *Geology* **43**:795-798.

Edgar, G. J., and R. D. Stuart-Smith. 2014. Systematic Global Assessment of Reef Fish Communities by the Reef Life Survey Program. *Scientific Data* **1**:140007.

Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, M. A. Becerro, A. T. Bernard, J. Berkhout, C. D. Buxton, S. J. Campbell, A. T. Cooper, M. Davey, S. C. Edgar, G. Forsterra, D. E. Galvan, A. J. Irigoyen, D. J. Kushner, R. Moura, P. E. Parnell, N. T. Shears, G. Soler, E. M. Strain, and R. J.

Thomson. 2014. Global Conservation Outcomes Depend on Marine Protected Areas with Five Key Features. *Nature* **506**:216-220.

Edwards, M., and A. J. Richardson. 2004. Impact of Climate Change on Marine Pelagic Phenology and Trophic Mismatch. *Nature* **430**:881.

Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677-697.

Elseberg, J., S. Magnenat, R. Siegwart, and A. Nüchter. 2012. Comparison of Nearest-Neighbor-Search Strategies and Implementations for Efficient Shape Registration. *Journal of Software Engineering for Robotics* **3**:2-12.

Evans, J. S. 2018. Spatialeco, R Package Version 0.1.1-1. https://CRAN.R-project.org/package=spatialEco.

FAO. 2016. Food and Agriculture Organization of the United Nations (Fao): The Eaf-Nansen Programme. Available At: Http://Www.Fao.Org/3/a-I6039e.Pdf. Last Accessed 26th May 2018. Accessed:

FAO. 2018. Food and Agriculture Organization of the United Nations (Fao): Ecosystem Approach. Available At: Http://Www.Fao.Org/Biodiversity/Cross-Sectoral-Issues/Ecosystem-Approach/En/. Last Accessed 26th May 2018. http://www.fao.org/biodiversity/cross-sectoral-issues/ecosystem-approach/en/. Accessed:

Fernández, D., R. Arnold, and S. Pledger. 2016. Mixture-Based Clustering for the Ordered Stereotype Model. *Computational Statistics & Data Analysis* **93**:46-75.

Ferrier, S., and A. Guisan. 2006. Spatial Modelling of Biodiversity at the Community Level. *Journal of Applied Ecology* **43**:393-404.

Fillinger, L., D. Janussen, T. Lundalv, and C. Richter. 2013. Rapid Glass Sponge Expansion after Climate-Induced Antarctic Ice Shelf Collapse. *Current Biology* **23**:1330-1334.

Fogwill, C. J., E. van Sebille, E. A. Cougnon, C. S. M. Turney, S. R. Rintoul, B. K. Galton-Fenzi, G. F. Clark, E. M. Marzinelli, E. B. Rainsley, and L. Carter. 2016. Brief Communication: Impacts of a Developing Polynya Off Commonwealth Bay, East Antarctica, Triggered by Grounding of Iceberg B09b. *The Cryosphere* **10**:2603-2609.

Fordham, D. A., T. M. L. Wigley, and B. W. Brook. 2011. Multi-Model Climate Projections for Biodiversity Risk Assessments. *Ecological Applications* **21**:3317-3331.

Foster, S. D., and P. K. Dunstan. 2010. The Analysis of Biodiversity Using Rank Abundance Distributions. *Biometrics* **66**:186-195.

Foster, S. D., P. K. Dunstan, F. Althaus, A. Williams, and A. Punt. 2015. The Cumulative Effect of Trawl Fishing on a Multispecies Fish Assemblage in South-Eastern Australia. *Journal of Applied Ecology* **52**:129-139.

Foster, S. D., G. H. Givens, G. J. Dornan, P. K. Dunstan, and R. Darnell. 2013. Modelling Biological Regions from Multi-Species and Environmental Data. *Environmetrics* **24**:489-499.

Foster, S. D., N. A. Hill, and M. Lyons. 2017. Ecological Grouping of Survey Sites When Sampling Artefacts Are Present. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* **66**:1031-1047.

Fraser, C. I., A. K. Morrison, A. M. Hogg, E. C. Macaya, E. van Sebille, P. G. Ryan, A. Padovan, C. Jack, N. Valdivia, and J. M. Waters. 2018. Antarctica's Ecological Isolation Will Be Broken by Storm-Driven Dispersal and Warming. *Nature Climate Change* **8**:704.

Fulton, E. A. 2010. Approaches to End-to-End Ecosystem Models. *Journal of Marine Systems* **81**:171-183.

Galton-Fenzi, B., J. Hunter, R. Coleman, S. Marsland, and R. Warner. 2012a. Numerical Modelling of Melt/Freeze beneath the Amery Ice Shelf. *Journal of Geophysical REsearch* **117**:C09031.

Galton-Fenzi, B. K., J. R. Hunter, R. Coleman, S. J. Marsland, and R. C. Warner. 2012b. Modeling the Basal Melting and Marine Ice Accretion of the Amery Ice Shelf. *Journal of Geophysical Research: Oceans* **117**.

Gambi, M. C., and S. Bussotti. 1999. Composition, Abundance and Stratification of Soft-Bottom Macrobenthos from Selected Areas of the Ross Sea Shelf (Antarctica). *Polar Biology* **21**:347-354.

Gamfeldt, L., J. S. Lefcheck, J. E. K. Byrnes, B. J. Cardinale, J. E. Duffy, and J. N. Griffin. 2015. Marine Biodiversity and Ecosystem Functioning: What's Known and What's Next? *Oikos* **124**:252-265.

Gaston, G. R. 1987. Benthic Polychaeta of the Middle Atlantic Bight: Feeding and Distribution. *Marine Ecology Progress Series* **36**:251-262.

Giles, A. B. 2017. The Mertz Glacier Tongue, East Antarctica. Changes in the Past 100 Years and Its Cyclic Nature - Past, Present and Future. *Remote Sensing of Environment* **191**:30-37.

Gillies, C. L., J. S. Stark, G. J. Johnstone, and S. D. A. Smith. 2013. Establishing a Food Web Model for Coastal Antarctic Benthic Communities: A Case Study from the Vestfold Hills. *Marine Ecology Progress Series* **478**:27-41.

Gillman, L. N., S. D. Wright, J. Cusens, P. D. McBride, Y. Malhi, and R. J. Whittaker. 2015. Latitude, Productivity and Species Richness. *Global Ecology and Biogeography* **24**:107-117.

Godınez-Domınguez, E., J. Rojo-Vázquez, V. Galvan-Pina, and B. Aguilar-Palomino. 2000. Changes in the Structure of a Coastal Fish Assemblage Exploited by a Small Scale Gillnet Fishery During an El Nino–La Nina Event. *Estuarine, Coastal and Shelf Science* **51**:773-787.

Gon, O., and P. C. Heemstra. 1990. Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology Grahamstown.

Goutx, M., S. G. Wakeham, C. Lee, M. Duflos, C. Guigue, Z. Liu, B. Moriceau, R. Sempéré, M. Tedetti, and J. Xue. 2007. Composition and Degradation of Marine Particles with Different Settling Velocities in the Northwestern Mediterranean Sea. *Limnology and Oceanography* **52**:1645.

Graf, G. 1989. Benthic-Pelagic Coupling in a Deep-Sea Benthic Community. *Nature* **341**:437-439.

Grand, J., M. P. Cummings, T. G. Rebelo, T. H. Ricketts, and M. C. Neel. 2007. Biased Data Reduce Efficiency and Effectiveness of Conservation Reserve Networks. *Ecology Letters* **10**:364-374.

Grant, S., A. Constable, B. Raymond, and S. Doust. 2006. Bioregionalisation of the Southern Ocean: Report of Experts Workshop, Hobart, September 2006., WWF-Australia and ACE CRC.

Grebmeier, J. M., and J. P. Barry. 1991. The Influence of Oceanographic Processes on Pelagic-Benthic Coupling in Polar Regions: A Bentic Perspective. *Journal of Marine Systems* **2**:495-518.

Griffiths, H. J. 2010. Antarctic Marine Biodiversity--What Do We Know About the Distribution of Life in the Southern Ocean? *PLoS One* **5**:e11683.

Griffiths, H. J., D. K. A. Barnes, and K. Linse. 2009. Towards a Generalized Biogeography of the Southern Ocean Benthos. *Journal of Biogeography* **36**:162-177.

Griffiths, H. J., A. J. S. Meijers, and T. J. Bracegirdle. 2017. More Losers Than Winners in a Century of Future Southern Ocean Seafloor Warming. *Nature Climate Change* **7**:749.

Guélat, J., and M. Kéry. 2018. Effects of Spatial Autocorrelation and Imperfect Detection on Species Distribution Models. *Methods in Ecology and Evolution* **9**:1614-1625.

Guisan, A., T. C. Edwards, and T. Hastie. 2002. Generalized Linear and Generalized Additive Models in Studies of Species Distributions: Setting the Scene. *Ecological Modelling* **157**:89-100.

Guisan, A., A. Lehmann, S. Ferrier, M. Austin, J. M. C. Overton, R. Aspinall, and T. Hastie. 2006. Making Better Biogeographical Predictions of Species' Distributions. *Journal of Applied Ecology* **43**:386-392.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T. G. Martin, J. R. Rhodes, R. Maggini, S. A. Setterfield, J. Elith, M. W. Schwartz, B. A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M. R. Kearney, H. P. Possingham, and Y. M. Buckley. 2013. Predicting Species Distributions for Conservation Decisions. *Ecology Letters* **16**:1424-1435.

Gurney, G. G., J. Melbourne-Thomas, R. C. Geronimo, P. M. Aliño, and C. R. Johnson. 2013. Modelling Coral Reef Futures to Inform Management: Can Reducing Local-Scale Stressors Conserve Reefs under Climate Change? *PLoS One* **8**:e80137.

Gutt, J. 2001. On the Direct Impact of Ice on Marine Benthic Commnities, a Review. *Polar Biology* **24**:553-564.

Gutt, J. 2007. Antarctic Macro-Zoobenthic Communities: A Review and an Ecological Classification. *Antarctic Science* **19**:165-182.

Gutt, J., D. Barnes, S. J. Lockhart, and A. van de Putte. 2013a. Antarctic Macrobenthic Communities: A compilation of circumpolar Information. *Nature Conservation* **4**:1-13.

Gutt, J., I. Barratt, E. Domack, C. D. d'Acoz, W. Dimmler, A. Gremare, O. Heilmayer, E. Isla, D. Janussen, E. Jorgensen, K. H. Kock, L. S. Lehnert, P. Lopez-Gonzales, S. Langner, K. Linse, M. E. Manjon-Cabeza, M. Meissner, A. Montiel, M. Raes, H. Robert, A. Rose, E. S. Schepisi, T. Saucede, M. Scheidat, H. W. Schenke, J. Seiler, and C. Smith. 2011. Biodiversity Change after Climate-Induced Ice-Shelf Collapse in the Antarctic. *Deep-Sea Research Part II: Topical Studies in Oceanography* **58**:74-83.

Gutt, J., N. Bertler, T. J. Bracegirdle, A. Buschmann, J. Comiso, G. Hosie, E. Isla, I. R. Schloss, C. R. Smith, and J. Tournadre. 2015. The Southern Ocean Ecosystem under Multiple Climate Change Stresses-an Integrated Circumpolar Assessment. *Global Change Biology* **21**:1434-1453.

Gutt, J., M. Cape, W. Dimmler, L. Fillinger, E. Isla, V. Lieb, T. Lundalv, and C. Pulcher. 2013b. Shifts in Antarctic Megabenthic Structure after Ice-Shelf Disintegration in the Larsen Area East of the Antarctic Peninsula. *Polar Biology* **36**:895-906.

Gutt, J., H. J. Griffiths, and C. D. Jones. 2013c. Circumpolar Overview and Spatial Heterogeneity of Antarctic Macrobenthic Communities. *Marine Biodiversity* **43**:481-487.

Gutt, J., P. Koubbi, and M. Eléaume. 2007. Mega-Epibenthic Diversity Off Terre Adélie (Antarctica) in Relation to Disturbance. *Polar Biology* **30**:1323-1329.

Gutt, J., B. I. Sirenko, I. S. Smirnov, and W. E. Arntz. 2004. How Many Macrozoobenthic Species Might Inhabit the Antarctic Shelf? *Antarctic Science* **16**:11-16.

Gutt, J., and A. Starmans. 1998. Structure and Biodiversity of Megabenthos in the Weddell and Lazarev Seas (Antarctica): Ecological Role of Physical Parameters and Biological Interactions. *Polar Biology* **20**:229-247.

Gutt, J., A. Starmans, and G. Dieckmann. 1996. Impact of Iceberg Scouring on Polar Benthic Habitats. *Marine Ecology Progress Series* **137**:311-316.

Gutt, J., D. Zurell, T. Bracegridle, W. Cheung, M. Clark, P. Convey, B. Danis, B. David, C. Broyer, G. Prisco, H. Griffiths, R. Laffont, L. Peck, B. Pierrat, M. Riddle, T. Saucède, J. Turner, C. Verde, Z. Wang, and V. Grimm. 2012. Correlative and Dynamic Species Distribution Modelling for Ecological Predictions in the Antarctic: A Cross-Disciplinary Concept. *Polar Research* **31**:11091.

Gwyther, D., B. Galton-Fenzi, J. Hunter, and J. Roberts. 2014. Simulated Melt Rates for the Totten and Dalton Ice Shelves. *Ocean Science* **10**:267.

Hanks, E. M., M. B. Hooten, S. T. Knick, S. J. Oyler-McCance, J. A. Fike, T. B. Cross, and M. K. Schwartz. 2016. Latent Spatial Models and Sampling Design for Landscape Genetics. *The Annals of Applied Statistics* **10**:1041-1062.

Harmelin‐Vivien, M. L., and P. Francour. 1992. Trawling or Visual Censuses? Methodological Bias in the Assessment of Fish Populations in Seagrass Beds. *Marine Ecology* **13**:41-51.

Harris, P. T., G. Brancolini, L. Armand, M. Busetti, R. J. Beaman, G. Giorgetti, M. Presti, and F. Trincardi. 2001. Continental Shelf Drift Deposit Indicates Non-Steady State Antarctic Bottom Water Production in the Holocene. *Marine Geology* **179**:1-8.

Harvey, C. J., J. C. Reum, M. R. Poe, G. D. Williams, and S. J. Kim. 2016. Using Conceptual Models and Qualitative Network Models to Advance Integrative Assessments of Marine Ecosystems. *Coastal Management* **44**:486-503.

Hauck, J., C. Görg, R. Varjopuro, O. Ratamäki, J. Maes, H. Wittmer, and K. Jax. 2013. "Maps Have an Air of Authority": Potential Benefits and Challenges of Ecosystem Service Maps at Different Levels of Decision Making. *Ecosystem Services* **4**:25-32.

Henson, S. A., R. Sanders, and E. Madsen. 2012. Global Patterns in Efficiency of Particulate Organic Carbon Export and Transfer to the Deep Ocean. *Global Biogeochemical Cycles* **26**:GB1028.

Heymans, J. J., M. Coll, J. S. Link, S. Mackinson, J. Steenbeek, C. Walters, and V. Christensen. 2016. Best Practice in Ecopath with Ecosim Food-Web Models for Ecosystem-Based Management. *Ecological Modelling* **331**:173-184.

Hijmans, R. J., and 2015. Raster: Geographic Data Analysis and Modeling.

Hill, N. A., S. D. Foster, G. Duhamel, D. Welsford, P. Koubbi, C. R. Johnson, and L. Hawkes. 2017. Model-Based Mapping of Assemblages for Ecology and Conservation Management: A Case Study of Demersal Fish on the Kerguelen Plateau. *Diversity and Distributions* **23**:1216-1230.

Hoegh-Guldberg, O., and J. F. Bruno. 2010a. The Impact of Climate Change on the World's Marine Ecosystems. *Science* **328**:1523-1528.

Hoegh-Guldberg, O., and J. F. Bruno. 2010b. The Impact of Climate Change on the World's Marine Ecosystems. *Science* **328**:1523-1528.

Hogg, O. T., V. A. Huvenne, H. J. Griffiths, B. Dorschel, and K. Linse. 2016. Landscape Mapping at Sub-Antarctic South Georgia Provides a Protocol for Underpinning Large-Scale Marine Protected Areas. *Scientific Reports* **6**:33163.

Holbrook, S. J., M. J. Kingsford, R. J. Schmitt, and J. S. Stephens Jr. 1994. Spatial and Temporal Patterns in Assemblages of Temperate Reef Fish. *American Zoologist* **34**:463-475.

Holland, D. M., and A. Jenkins. 1999. Modeling Thermodynamic Ice–Ocean Interactions at the Base of an Ice Shelf. *Journal of Physical Oceanography* **29**:1787-1800.

Hosie, G., P. Koubbi, M. Riddle, C. Ozouf-Costaz, M. Moteki, M. Fukuchi, N. Ameziane, T. Ishimaru, and A. Goffart. 2011. Ceamarc, the Collaborative East Antarctic Marine Census for the Census of Antarctic Marine Life (Ipy # 53): An Overview. *Polar Science* **5**:75-87.

Huang, K., H. Ducklow, M. Vernet, N. Cassar, and M. L. Bender. 2012. Export Production and Its Regulating Factors in the West Antarctica Peninsula Region of the Southern Ocean. *Global Biogeochemical Cycles* **26**.

Hui, F. K., S. Taskinen, S. Pledger, S. D. Foster, and D. I. Warton. 2015. Model‐Based Approaches to Unconstrained Ordination. *Methods in Ecology and Evolution* **6**:399-411.

Hui, F. K. C., D. I. Warton, S. D. Foster, and P. K. Dunstan. 2013. To Mix or Not to Mix: Comparing the Predictive Performance of Mixture Models Vs. Separate Species Distribution Models. *Ecology* **94**:1913-1919.

Isaac, N. J., and M. J. Pocock. 2015. Bias and Information in Biological Records. *Biological Journal of the Linnean Society* **115**:522-531.

Jahnke, R. A., C. E. Reimers, and D. B. Craven. 1990. Intensification of Recycling of Organic Matter at the Sea Floor near Ocean Margins. *Nature* **348**:50-54.

Jansen, J. 2018. Environmental Data Layers for a 5 Year Period before and after the Calving of the Mertz Glacier Tongue. *Australian Antarctic Data Centre - CAASM Metadata*. http://dx.doi.org/doi:10.4225/15/5ab85fcdc226e

Jansen, J., N. A. Hill, P. K. Dunstan, E. A. Cougnon, B. K. Galton-Fenzi, and C. R. Johnson. 2018a. Mapping Antarctic Suspension Feeder Abundances and Seafloor Food-Availability, and Modeling Their Change after a Major Glacier Calving. *Frontiers in Ecology and Evolution* **6**:94.

Jansen, J., N. A. Hill, P. K. Dunstan, M. P. Eléaume, and C. R. Johnson. 2018b. Taxonomic Resolution, Functional Traits, and the Influence of Species Groupings on Mapping Antarctic Seafloor Biodiversity. *Frontiers in Ecology and Evolution* **6**:81.

Jansen, J., N. A. Hill, P. K. Dunstan, J. McKinlay, M. D. Sumner, A. L. Post, M. P. Eleaume, L. K. Armand, J. P. Warnock, B. K. Galton-Fenzi, and C. R. Johnson. 2018c. Abundance and Richness of Key Antarctic Seafloor Fauna Correlates with Modelled Food Availability. *Nature Ecology and Evolution* **2**:71-80.

Jansen, J., C. Robineau, J. Delaplanque-Lasserre, and M. Eleaume. 2017. Abundances of Broad Benthic Functional Groups in the Ceamarc Region 2007/08. *Australian Antarctic Data Centre*. http://dx.doi.org/doi:10.4225/15/59dea9a19a61d

Jansen, J., and M. D. Sumner. 2017. Ptrackr: R-Package for Tracking Individual Particles in Two- and Three-Dimensional Space. *Zenodo*. http://doi.org/10.5281/zenodo.803493

Johnson, R., P. G. Strutton, S. W. Wright, A. McMinn, and K. M. Meiners. 2013. Three Improved Satellite Chlorophyll Algorithms for the Southern Ocean. *Journal of Geophysical Research: Oceans* **118**:3694-3703.

Jones, D. O., A. Yool, C. L. Wei, S. A. Henson, H. A. Ruhl, R. A. Watson, and M. Gehlen. 2014. Global Reductions in Seafloor Biomass in Response to Climate Change. *Global Change Biology* **20**:1861-1872.

Jones, J. P. 2011. Monitoring Species Abundance and Distribution at the Landscape Scale. *Journal of Applied Ecology* **48**:9-13.

Jones, T. 2017. Commission for the Conservation of Antarctic Marine Living Resources: Vulnerable Marine Ecosystems Registry. www.ccamlr.org/en/document/data/ccamlr-vme-registry. Accessed: 28.05.2018

Jordan, A., M. Lawler, V. Halley, and N. Barrett. 2005. Seabed Habitat Mapping in the Kent Group of Islands and Its Role in Marine Protected Area Planning. *Aquatic Conservation: Marine and Freshwater Ecosystems* **15**:51-70.

Keith, D. A. 2015. Assessing and Managing Risks to Ecosystem Biodiversity. *Austral Ecology* **40**:337-346.

Kock, K. H. 2007. Antarctic Marine Living Resources – Exploitation and Its Management in the Southern Ocean. *Antarctic Science* **19**:231-238.

Koubbi, P., G. Hosie, A. Constable, B. Raymond, M. Moteki, N. Améziane, R. Causse, V. Fuentes, K. Heerah, F. Penot, D. Vincent, A. Ancel, C. A. Bost, M. Eléaume, D. Lindsay, M. Lindsay, M. Cottin, J. B. Charrassin, Y. Ropert-Coudert, R. Toda, M. Grossmann, R. Hopcroft, C. Ozouf-Costaz, I. Zimmer, and CEAMARC-experts. 2011a. Estimating the Biodiversity of the Shelf and Oceanic Zone of the D'urville Sea (East Antarctica) for Ecoregionalisation Using the Ceamarc (Collaborative East Antarctic Marine Census) Caml Surveys.

Koubbi, P., M. Moteki, G. Duhamel, A. Goarant, P. A. Hulley, R. O'Driscoll, T. Ishimaru, P. Pruvost, E. Tavernier, and G. Hosie. 2011b. Ecoregionalization of Myctophid Fish in the Indian Sector of the Southern Ocean: Results from Generalized Dissimilarity Models. *Deep-Sea Research Part II: Topical Studies in Oceanography* **58**:170-180.

Koubbi, P., C. Ozouf-Costaz, A. Goarant, M. Moteki, P.-A. Hulley, R. Causse, A. Dettai, G. Duhamel, P. Pruvost, E. Tavernier, A. L. Post, R. J. Beaman, S. R. Rintoul, T. Hirawake, D. Hirano, T. Ishimaru, M. Riddle, and G. Hosie. 2010. Estimating the Biodiversity of the East Antarctic Shelf and Oceanic Zone for Ecoregionalisation: Example of the Ichthyofauna of the Ceamarc (Collaborative East Antarctic Marine Census) Caml Surveys. *Polar Science* **4**:115-133.

Kröger, K., and A. A. Rowden. 2008. Polychaete Assemblages of the Northwestern Ross Sea Shelf: Worming out the Environmental Drivers of Antarctic Macrobenthic Assemblage Composition. *Polar Biology* **31**:971-989.

Kusahara, K., H. Hasumi, A. D. Fraser, S. Aoki, K. Shimada, G. D. Williams, R. Massom, and T. Tamura. 2017. Modeling Ocean–Cryosphere Interactions Off Adélie and George V Land, East Antarctica. *Journal of Climate* **30**:163-188.

Lacharité, M., and A. Metaxas. 2017. Hard Substrate in the Deep Ocean: How Sediment Features Influence Epibenthic Megafauna on the Eastern Canadian Margin. *Deep-Sea Research Part I: Oceanographic Research Papers* **126**:50-61.

Lagabrielle, Y., Y. Goddéris, Y. Donnadieu, J. Malavieille, and M. Suarez. 2009. The Tectonic History of Drake Passage and Its Possible Impacts on Global Climate. *Earth and Planetary Science Letters* **279**:197-211.

Lampitt, R. 1985. Evidence for the Seasonal Deposition of Detritus to the Deep-Sea Floor and Its Subsequent Resuspension. *Deep-Sea Research Part I: Oceanographic Research Papers* **32**:885-897.

Laufkötter, C., M. Vogt, N. Gruber, M. Aita-Noguchi, O. Aumont, L. Bopp, E. Buitenhuis, S. C. Doney, J. Dunne, T. Hashioka, J. Hauck, T. Hirata, J. John, C. Le Quéré, I. D. Lima, H. Nakano, R. Seferian, I. Totterdell, M. Vichi, and C. Völker. 2015. Drivers and Uncertainties of Future Global Marine Primary Production in Marine Ecosystem Models. *Biogeosciences* **12**:6955-6984.

Laurenceau-Cornec, E. C., T. W. Trull, D. M. Davies, C. L. De La Rocha, and S. Blain. 2015. Phytoplankton Morphology Controls on Marine Snow Sinking Velocity. *Marine Ecology Progress Series* **520**:35-56.

Laws, E. A., P. G. Falkowski, W. O. Smith, H. Ducklow, and J. J. McCarthy. 2000. Temperature Effects on Export Production in the Open Ocean. *Global Biogeochemical Cycles* **14**:1231-1246.

Lawver, L. A., and L. M. Gahagan. 2003. Evolution of Cenozoic Seaways in the Circum-Antarctic Region. *Palaeogeography, Palaeoclimatology, Palaeoecology* **198**:11-37.

Learman, D. R., M. W. Henson, J. C. Thrash, B. Temperton, P. M. Brannock, S. R. Santos, A. R. Mahon, and K. M. Halanych. 2016. Biogeochemical and Microbial Variation across 5500 Km of Antarctic Surface Sediment Implicates Organic Matter as a Driver of Benthic Community Structure. *Frontiers in Microbiology* **7**:284.

Lecours, V., R. Devillers, V. L. Lucieer, and C. J. Brown. 2017. Artefacts in Marine Digital Terrain Models: A Multiscale Analysis of Their Impact on the Derivation of Terrain Attributes. *IEEE Transactions on Geoscience and Remote Sensing* **55**:5391-5406.

Lehmann, A., J. M. Overton, and M. P. Austin. 2002. Regression Models for Spatial Prediction: Their Role for Biodiversity and Conservation. *Biodiversity and Conservation* **11**:2085-2092.

Levins, R. 1966. The Strategy of Model Building in Population Biology. *American Scientist* **54**:421-431.

Levins, R. 1993. A Response to Orzack and Sober: Formal Analysis and the Fluidity of Science. *The Quarterly Review of Biology* **68**:547-555.

Lins, L., M. C. da Silva, F. Hauquier, A. M. Esteves, and A. Vanreusel. 2015. Nematode Community Composition and Feeding Shaped by Contrasting Productivity Regimes in the Southern Ocean. *Progress in Oceanography* **134**:356-369.

Lombarte, A., I. Olaso, and A. Bozzano. 2003. Ecomorphological Trends in the Artedidraconidae (Pisces: Perciformes: Notothenioidei) of the Weddell Sea. *Antarctic Science* **15**:211-218.

Lutz, M. J., K. Caldeira, R. B. Dunbar, and M. J. Behrenfeld. 2007. Seasonal Rhythms of Net Primary Production and Particulate Organic Carbon Flux to Depth Describe the Efficiency of Biological Pump in the Global Ocean. *Journal of Geophysical Research: Oceans* **112**.

Marzloff, M. P., L. R. Little, and C. R. Johnson. 2015. Building Resilience against Climate-Driven Shifts in a Temperate Reef System: Staying Away from Context-Dependent Ecological Thresholds. *Ecosystems* **19**:1-15.

Marzloff, M. P., E. C. J. Oliver, N. S. Barrett, N. J. Holbrook, L. James, S. J. Wotherspoon, and C. R. Johnson. 2018. Differential Vulnerability to Climate Change Yields Novel Deep-Reef Communities. *Nature Climate Change* **8**:873-878.

Massom, R., K. Hill, V. Lytle, A. Worby, M. Paget, and I. Allison. 2001. Effects of Regional Fast-Ice and Iceberg Distributions on the Behaviour of the Mertz Glacier Polynya, East Antarctica. *Annals of Glaciology* **33**:391-398.

Mayer, L., M. Jakobsson, G. Allen, B. Dorschel, R. Falconer, V. Ferrini, G. Lamarche, H. Snaith, and P. Weatherall. 2018. The Nippon Foundation—Gebco Seabed 2030 Project: The Quest to See the World's Oceans Completely Mapped by 2030. *Geosciences* **8**.

Mayet, C., L. Testut, B. Legresy, L. Lescarmontier, and F. Lyard. 2013. High-Resolution Barotropic Modeling and the Calving of the Mertz Glacier, East Antarctica. *Journal of Geophysical Research: Oceans* **118**:5267-5279.

McCave, I. N., and S. A. Swift. 1976. A Physical Model for the Rate of Deposition of Fine-Grained Sediments in the Deep Sea. *Geological Society of America Bulletin* **87**:541-546.

McConnell, B., C. Chambers, and M. Fedak. 1992. Foraging Ecology of Southern Elephant Seals in Relation to the Bathymetry and Productivity of the Southern Ocean. *Antarctic Science* **4**:393-398.

Mccoy, F. W. 1991. Southern Ocean Sediments: Circum-Antarctic to 30°S. Pages 37-46 Marine Geological and Geophysical Atlas of the Circum-Antarctic to 30°S. American Geophysical Union.

Melbourne-Thomas, J., A. Constable, S. Wotherspoon, and B. Raymond. 2013. Testing Paradigms of Ecosystem Change under Climate Warming in Antarctica. *PLoS One* **8**:e55093.

Melbourne-Thomas, J., C. Johnson, P. Alino, R. C. Geronimo, C. Villanoy, and G. Gurney. 2011a. A Multi-Scale Biophysical Model to Inform Regional Management of Coral Reefs in the Western Philippines and South China Sea. *Environmental Modelling & Software* **26**:66-82.

Melbourne-Thomas, J., C. R. Johnson, T. Fung, R. M. Seymour, L. M. Chérubin, J. E. Arias-González, and E. A. Fulton. 2011b. Regional-Scale Scenario Modeling for Coral Reefs: A Decision Support Tool to Inform Management of a Complex System. *Ecological Applications* **21**:1380-1398.

Melbourne-Thomas, J., S. Wotherspoon, B. Raymond, and A. Constable. 2012. Comprehensive Evaluation of Model Uncertainty in Qualitative Network Analyses. *Ecological Monographs* **82**:505-519.

NASA Goddard Space Flight Center, O. E. L., Ocean Biology Processing Group: MODIS-Aqua Ocean Color Data. 2014. http://dx.doi.org/10.5067/AQUA/MODIS_OC.2014.0

O'Hara, T. D., A. A. Rowden, and N. J. Bax. 2011. A Southern Hemisphere Bathyal Fauna Is Distributed in Latitudinal Bands. *Current Biology* **21**:226-230.

OAO. 2018. Oceanographic Autonomous Observations (Oao): Bio Argo. http://www.oao.obs-vlfr.fr/web/index.php/projects/other-ongoing-projetcs/108-bio-argo. Accessed: 01.10.2018

Obermüller, B. E., S. A. Morley, D. K. Barnes, and L. S. Peck. 2010. Seasonal Physiology and Ecology of Antarctic Marine Benthos Predators and Scavengers. *Marine Ecology Progress Series* **415**:109-126.

Orr, J. C., V. J. Fabry, O. Aumont, L. Bopp, S. C. Doney, R. A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, R. M. Key, K. Lindsay, E. Maier-Reimer, R. Matear, P. Monfray, A. Mouchet, R. G. Najjar, G. K. Plattner, K. B. Rodgers, C. L. Sabine, J. L. Sarmiento, R. Schlitzer, R. D. Slater, I. J. Totterdell, M. F. Weirig, Y.

Yamanaka, and A. Yool. 2005. Anthropogenic Ocean Acidification over the Twenty-First Century and Its Impact on Calcifying Organisms. *Nature* **437**:681-686.

Ovaskainen, O., and J. Soininen. 2011. Making More out of Sparse Data: Hierarchical Modeling of Species Communities. *Ecology* **92**:289-295.

Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin, and N. Abrego. 2017. How to Make More out of Community Data? A Conceptual Framework and Its Implementation as Models and Software. *Ecology Letters* **20**:561-576.

Parkinson, C., and D. Cavalieri. 2012. Antarctic Sea Ice Variability and Trends, 1979–2010. *The Cryosphere* **6**:871-880.

Peck, L. S., D. K. Barnes, A. J. Cook, A. H. Fleming, and A. Clarke. 2010. Negative Feedback in the Cold: Ice Retreat Produces New Carbon Sinks in Antarctica. *Global Change Biology* **16**:2614-2623.

Peck, L. S., K. E. Webb, and D. M. Bailey. 2004. Extreme Sensitivity of Biological Function to Temperature in Antarctic Marine Species. *Functional Ecology* **18**:625-630.

Pecl, G., Y. Barry, R. Brown, S. Frusher, E. Gartner, A. Pender, L. Robinson, P. Walsh, and J. Stuart-Smith. 2014. Redmap: Ecological Monitoring and Community Engagement through Citizen Science. *Tasmanian naturalist* **136**:158-164.

Pennekamp, F., M. Pontarp, A. Tabi, F. Altermatt, R. Alther, Y. Choffat, E. A. Fronhofer, P. Ganesanandamoorthy, A. Garnier, J. I. Griffiths, S. Greene, K. Horgan, T. M. Massie, E. Machler, G. M. Palamara, M. Seymour, and O. L. Petchey. 2018. Biodiversity Increases and Decreases Ecosystem Stability. *Nature* **563**:109-112.

Petchey, O. L., and K. J. Gaston. 2006. Functional Diversity: Back to Basics and Looking Forward. *Ecology Letters* **9**:741-758.

Pierce, D., and 2014. Ncdf4: Interface to Unidata Netcdf (Version 4 or Earlier) Format Data Files. .

Pierrat, B., T. Saucède, R. Laffont, C. De Ridder, A. Festeau, and B. David. 2012. Large-Scale Distribution Analysis of Antarctic Echinoids Using Ecological Niche Modelling. *Marine Ecology Progress Series* **463**:215-230.

Pirotta, E., J. Matthiopoulos, M. MacKenzie, L. Scott-Hayward, and L. Rendell. 2011. Modelling Sperm Whale Habitat Preference: A Novel Approach Combining Transect and Follow Data. *Marine Ecology Progress Series* **436**:257-272.

Pledger, S., and R. Arnold. 2014. Multivariate Methods Using Mixtures: Correspondence Analysis, Scaling and Pattern-Detection. *Computational Statistics & Data Analysis* **71**:241-261.

Post, A. L., R. J. Beaman, P. E. O'Brien, M. Eleaume, and M. J. Riddle. 2011. Community Structure and Benthic Habitats across the George V Shelf, East Antarctica: Trends through Space and Time. *Deep-Sea Research Part II: Topical Studies in Oceanography* **58**:105-118.

Post, A. L., C. Lavoie, E. W. Domack, A. Leventer, A. Shevenell, and A. D. Fraser. 2017. Environmental Drivers of Benthic Communities and Habitat Heterogeneity on an East Antarctic Shelf. *Antarctic Science* **29**:17-32.

Post, A. L., A. J. S. Meijers, A. D. Fraser, K. M. Meiners, J. Ayers, N. L. Bindoff, H. J. Griffiths, A. P. Van de Putte, P. E. O'Brien, K. M. Swadling, and B. Raymond. 2014. Chapter 4. Environmental Setting. Pages 46-64 *in* C. De Broyer, P. Koubbi, H. J. Griffiths, B. Raymond, C. d. Udekem d'Acoz, A. P. Van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Huettmann, A. Post, and Y. Ropert-Coudert, (eds). Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge.

Post, A. L., P. E. O'Brien, R. J. Beaman, M. J. Riddle, and L. De Santis. 2010. Physical Controls on Deep Water Coral Communities on the George V Land Slope, East Antarctica. *Antarctic Science* **22**:371-378.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rathburn, A. E., J. J. Pichon, M. A. Ayress, and P. DeDeckker. 1997. Microfossil and Stable-Isotope Evidence for Changes in Late Holocene Paleoproductivity and Paleoceanographic Conditions in the Prydz Bay Region of Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **131**:485-510.

Raymond, B. 2011. A Circumpolar Pelagic Regionalisation of the Southern Ocean.*in* CCAMLR Workshop on Marine Protected Areas.

Raymond, B., J. McInnes, J. M. Dambacher, S. Way, and D. M. Bergstrom. 2011. Qualitative Modelling of Invasive Species Eradication on Subantarctic Macquarie Island. *Journal of Applied Ecology* **48**:181-191.

Rehm, P., S. Thatje, W. E. Arntz, A. Brandt, and O. Heilmayer. 2006. Distribution and Composition of Macrozoobenthic Communities Along a Victoria-Land Transect (Ross Sea, Antarctica). *Polar Biology* **29**:782-790.

Renaud, P. E., N. Morata, M. L. Carroll, S. G. Denisenko, and M. Reigstad. 2008. Pelagic–Benthic Coupling in the Western Barents Sea: Processes and Time Scales. *Deep-Sea Research Part II: Topical Studies in Oceanography* **55**:2372-2380.

Reyers, B., M. Rouget, Z. Jonas, R. Cowling, A. Driver, K. Maze, and P. Desmet. 2007. Developing Products for Conservation Decision‐Making: Lessons from a Spatial Biodiversity Assessment for South Africa. *Diversity and Distributions* **13**:608-619.

Rigual-Hernández, A. S., T. W. Trull, S. G. Bray, I. Closset, and L. K. Armand. 2015. Seasonal Dynamics in Diatom and Particulate Export Fluxes to the Deep Sea in the Australian Sector of the Southern Antarctic Zone. *Journal of Marine Systems* **142**:62-74.

Riser, S. C., H. J. Freeland, D. Roemmich, S. Wijffels, A. Troisi, M. Belbéoch, D. Gilbert, J. Xu, S. Pouliquen, A. Thresher, P.-Y. Le Traon, G. Maze, B. Klein, M. Ravichandran, F. Grant, P.-M. Poulain, T. Suga, B. Lim, A. Sterl, P. Sutton, K.-A. Mork, P. J. Vélez-Belchí, I. Ansorge, B. King, J. Turton, M. Baringer, and S. R. Jayne. 2016. Fifteen Years of Ocean Observations with the Global Argo Array. *Nature Climate Change* **6**:145.

Roberts, J. M., A. J. Wheeler, and A. Freiwald. 2006. Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. *Science* **312**:543-547.

Robineau, C., J. Delaplanque-Lasserre, J. Jansen, and M. Eleaume. 2018. Abundances of Benthic Invertebrate Species in the Ceamarc Region 2007/08 *Australian Antarctic Data Centre - CAASM Metadata*. http://dx.doi.org/doi:10.4225/15/5ae7cf565cebb

Rooker, J., and G. Dennis. 1991. Diel, Lunar and Seasonal Changes in a Mangrove Fish Assemblage Off Southwestern Puerto Rico. *Bulletin of Marine Science* **49**:684-698.

Rooper, C. N., M. Zimmermann, M. M. Prescott, and A. J. Hermann. 2014. Predictive Models of Coral and Sponge Distribution, Abundance and Diversity in Bottom Trawl Surveys of the Aleutian Islands, Alaska. *Marine Ecology Progress Series* **503**:157-176.

Ruhl, H. A., B. J. Bett, S. J. M. Hughes, C. H. S. Alt, E. J. Ross, R. S. Lampitt, C. A. Pebody, K. L. Smith, and D. S. M. Billett. 2014. Links between Deep-Sea Respiration and Community Dynamics. *Ecology* **95**:1651-1662.

Saenz, B. T., and K. R. Arrigo. 2014. Annual Primary Production in Antarctic Sea Ice During 2005-2006 from a Sea Ice State Estimate. *Journal of Geophysical Research: Oceans* **119**:3645-3678.

Saildrone. 2018. http://www.saildrone.com/. Accessed: 01.10.2018

Sambrotto, R. N., A. Matsuda, R. Vaillancourt, M. Brown, C. Langdon, S. S. Jacobs, and C. Measures. 2003. Summer Plankton Production and Nutrient Consumption Patterns in the Mertz Glacier Region of East Antarctica. *Deep-Sea Research Part II: Topical Studies in Oceanography* **50**:1393-1414.

SCBD. 2012. Report of the High-Level Panel on Global Assessment of Resources for Implementing the Strategic Plan for Biodiversity 2011–2020 (No. Unep/Cbd/Cop/11/Inf/20). Secretariat of the Convention on Biological Diversity (SCBD), Montreal, Canada.

Shadwick, E. H., S. R. Rintoul, B. Tilbrook, G. D. Williams, N. Young, A. D. Fraser, H. Marchant, J. Smith, and T. Tamura. 2013. Glacier Tongue Calving Reduced Dense Water Formation and Enhanced Carbon Uptake. *Geophysical Research Letters* **40**:904-909.

Sharp, B. R., S. J. Parker, M. H. Pinkerton, B. B. Breen, V. Cummings, A. Dunne, S. M. Grant, S. M. Hanchet, H. J. R. Keys, S. J. Lockhart, P. O. B. Lyver, R. L. O'Driscoll, M. J. M. Williams, and W. P. R. 2010. Bioregionalisation and Spatial Ecosystem Processes in the Ross Sea Region. Working Group on Ecosystem Monitoring and Management-10/30., Commission for the Conservation of Antarctic Marine Living Resources.

Shchepetkin, A. F., and J. C. McWilliams. 2005. The Regional Oceanic Modeling System (Roms): A Split-Explicit, Free-Surface, Topography-Following-Coordinate Oceanic Model. *Ocean Modelling* **9**:347-404.

Siegel, D. A., K. O. Buesseler, S. C. Doney, S. F. Sailley, M. J. Behrenfeld, and P. W. Boyd. 2014. Global Assessment of Ocean Carbon Export by Combining Satellite Observations and Food-Web Models. *Global Biogeochemical Cycles* **28**:181-196.

Smale, D. A., G. A. Kendrick, and T. Wernberg. 2010. Assemblage Turnover and Taxonomic Sufficiency of Subtidal Macroalgae at Multiple Spatial Scales. *Journal of Experimental Marine Biology and Ecology* **384**:76-86.

Smith, C. R., S. Mincks, and D. J. DeMaster. 2006. A Synthesis of Bentho-Pelagic Coupling on the Antarctic Shelf: Food Banks, Ecosystem Inertia and Global Climate Change. *Deep-Sea Research Part II: Topical Studies in Oceanography* **53**:875-894.

Smith, C. R., S. Mincks, and D. J. DeMaster. 2008. The Foodbancs Project: Introduction and Sinking Fluxes of Organic Carbon, Chlorophyll-a and Phytodetritus on the Western Antarctic Peninsula Continental Shelf. *Deep-Sea Research Part II: Topical Studies in Oceanography* **55**:2404-2414.

Stewart, A. L., A. Klocker, and D. Menemenlis. 2018. Circum-Antarctic Shoreward Heat Transport Derived from an Eddy- and Tide-Resolving Simulation. *Geophysical Research Letters* **45**:834-845.

Stuart-Smith, R. D., A. E. Bates, J. S. Lefcheck, J. E. Duffy, S. C. Baker, R. J. Thomson, J. F. Stuart-Smith, N. A. Hill, S. J. Kininmonth, L. Airoldi, M. A. Becerro, S. J. Campbell, T. P. Dawson, S. A. Navarrete, G. A. Soler, E. M. Strain, T. J. Willis, and G. J. Edgar. 2013. Integrating Abundance and Functional Traits Reveals New Global Hotspots of Fish Diversity. *Nature* **501**:539-542.

Stuart-Smith, R. D., C. J. Brown, D. M. Ceccarelli, and G. J. Edgar. 2018. Ecosystem Restructuring Along the Great Barrier Reef Following Mass Coral Bleaching. *Nature* **560**:92.

Stuart-Smith, R. D., G. J. Edgar, N. S. Barrett, S. J. Kininmonth, and A. E. Bates. 2015. Thermal Biases and Vulnerability to Warming in the World's Marine Fauna. *Nature* **528**:88-92.

Suess, E. 1980. Particulate Organic-Carbon Flux in the Oceans - Surface Productivity and Oxygen Utilization. *Nature* **288**:260-263.

Sunday, J. M., G. T. Pecl, S. Frusher, A. J. Hobday, N. Hill, N. J. Holbrook, G. J. Edgar, R. Stuart-Smith, N. Barrett, T. Wernberg, R. A. Watson, D. A. Smale, E. A. Fulton, D. Slawinski, M. Feng, B. T. Radford, P. A. Thompson, and A. E. Bates. 2015a. Species Traits and Climate Velocity Explain Geographic Range Shifts in an Ocean-Warming Hotspot. *Ecology Letters* **18**:944-953.

Sunday, J. M., G. T. Pecl, S. Frusher, A. J. Hobday, N. Hill, N. J. Holbrook, G. J. Edgar, R. Stuart-Smith, N. Barrett, and T. Wernberg. 2015b. Species Traits and Climate Velocity Explain Geographic Range Shifts in an Ocean-Warming Hotspot. *Ecology Letters* **18**:944-953.

Sutcliffe, P. R., C. R. Pitcher, M. J. Caley, and H. P. Possingham. 2012. Biological Surrogacy in Tropical Seabed Assemblages Fails. *Ecological Applications* **22**:1762-1771.

Swingland, I. R. 2001. Biodiversity, Definition Of. *Encyclopedia of biodiversity* **1**:377-391.

Takahashi, A., M. Dunn, P. Trathan, K. Sato, Y. Naito, and J. Croxall. 2003. Foraging Strategies of Chinstrap Penguins at Signy Island, Antarctica: Importance of Benthic Feeding on Antarctic Krill. *Marine Ecology Progress Series* **250**:279-289.

Tamura, T., K. I. Ohshima, A. D. Fraser, and G. D. Williams. 2016. Sea Ice Production Variability in Antarctic Coastal Polynyas. *Journal of Geophysical Research: Oceans* **121**:2967-2979.

Tamura, T., G. D. Williams, A. D. Fraser, and K. I. Ohshima. 2012. Potential Regime Shift in Decreased Sea Ice Production after the Mertz Glacier Calving. *Nature Communications* **3**:826.

Tarr, G., S. Müller, and A. Welsh. 2015. Mplot: An R Package for Graphical Model Stability and Variable Selection Procedures. *arXiv preprint arXiv:1509.07583*.

Terlizzi, A., M. J. Anderson, S. Bevilacqua, S. Fraschetti, M. Włodarska-Kowalczuk, and K. E. Ellingsen. 2009. Beta Diversity and Taxonomic Sufficiency: Do Higher-Level Taxa Reflect Heterogeneity in Species Composition? *Diversity and Distributions* **15**:450-458.

Thrush, S. F., J. E. Hewitt, V. J. Cummings, A. Norkko, and M. Chiantore. 2010. Beta-Diversity and Species Accumulation in Antarctic Coastal Benthos: Influence of Habitat, Distance and Productivity on Ecological Connectivity. *PLoS One* **5**:e11899.

Thurber, A. R., A. K. Sweetman, B. E. Narayanaswamy, D. O. B. Jones, J. Ingels, and R. L. Hansman. 2014. Ecosystem Function and Services Provided by the Deep Sea. *Biogeosciences* **11**:3941-3963.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**:471-493.

Timmermann, R., A. Le Brocq, T. Deen, E. Domack, P. Dutrieux, B. Galton-Fenzi, H. Hellmer, A. Humbert, D. Jansen, A. Jenkins, A. Lambrecht, K. Makinson, F. Niederjasper, F. Nitsche, O. A. Nøst, L. H. Smedsrud, and W. H. F. Smith. 2010. A Consistent Data Set of Antarctic Ice Sheet Topography, Cavity Geometry, and Global Bathymetry. *Earth System Science Data* **2**:261-273.

Tomas, C. R. 1997. Identifying Marine Phytoplankton. Academic Press, San Diego.

Tremblay, Y., and Y. Cherel. 2000. Benthic and Pelagic Dives: A New Foraging Behaviour in Rockhopper Penguins. *Marine Ecology Progress Series* **204**:257-267.

Van Ierland, E., and L. Peperzak. 1984. Separation of Marine Seston and Density Determination of Marine Diatoms by Density Gradient Centrifugation. *Journal of Plankton Research* **6**:29-44.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Springer, New York.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological Responses to Recent Climate Change. *Nature* **416**:389-395.

Warner, J. C., C. R. Sherwood, R. P. Signell, C. K. Harris, and H. G. Arango. 2008. Development of a Three-Dimensional, Regional, Coupled Wave, Current, and Sediment-Transport Model. *Computers & Geosciences* **34**:1284-1306.

Warton, D. I., F. G. Blanchet, R. B. O'Hara, O. Ovaskainen, S. Taskinen, S. C. Walker, and F. K. C. Hui. 2015a. So Many Variables: Joint Modeling in Community Ecology. *Trends in Ecology and Evolution* **30**:766-779.

Warton, D. I., S. D. Foster, G. De'ath, J. Stoklosa, and P. K. Dunstan. 2015b. Model-Based Thinking for Community Ecology. *Plant Ecology* **216**:669-682.

Warton, D. I., I. W. Renner, and D. Ramp. 2013. Model-Based Control of Observer Bias for the Analysis of Presence-Only Data in Ecology. *PLoS One* **8**:e79168.

Warton, D. I., S. T. Wright, and Y. Wang. 2012. Distance-Based Multivariate Analyses Confound Location and Dispersion Effects. *Methods in Ecology and Evolution* **3**:89-101.

Watling, L., J. Guinotte, M. R. Clark, and C. R. Smith. 2013. A Proposed Biogeography of the Deep Ocean Floor. *Progress in Oceanography* **111**:91-112.

Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A Structured and Dynamic Framework to Advance Traits-Based Theory and Prediction in Ecology. *Ecology Letters* **13**:267-283.

Wei, C. L., G. T. Rowe, G. F. Hubbard, A. H. Scheltema, G. D. F. Wilson, I. Petrescu, J. M. Foster, M. K. Wicksten, M. Chen, R. Davenport, Y. Soliman, and Y. Wang. 2010. Bathymetric Zonation of Deep-Sea Macrofauna in Relation to Export of Surface Phytoplankton Production. *Marine Ecology Progress Series* **399**:1-14.

Welsford, D. C., G. P. Ewing, A. J. Constable, T. Hibbert, and R. Kilpatrick. 2014. Demersal Fishing Interactions with Marine Benthos in the Australian Eez of the Southern Ocean: An Assessment of the Vulnerability of Benthic Habitats to Impact by Demersal Gears.

Wilkinson, M. D., M. Dumontier, I. J. Aalbersberg, G. Appleton, M. Axton, A. Baak, N. Blomberg, J.-W. Boiten, L. B. da Silva Santos, and P. E. Bourne. 2016. The Fair Guiding Principles for Scientific Data Management and Stewardship. *Scientific Data* **3**.

Williams, G. D., N. L. Bindoff, S. J. Marsland, and S. R. Rintoul. 2008. Formation and Export of Dense Shelf Water from the Adélie Depression, East Antarctica. *Journal of Geophysical REsearch* **113**:C04039.

Wilson, K.-J., C. S. M. Turney, C. J. Fogwill, and E. Blair. 2016. The Impact of the Giant Iceberg B09b on Population Size and Breeding Success of Adélie Penguins in Commonwealth Bay, Antarctica. *Antarctic Science* **28**:187-193.

Wodarska-Kowalczuk, M., and M. Kedra. 2007. Surrogacy in Natural Patterns of Benthic Distribution and Diversity: Selected Taxa Versus Lower Taxonomic Resolution. *Marine Ecology Progress Series* **351**:53-63.

Woolley, S. N. C., A. W. McCallum, R. Wilson, T. D. O'Hara, P. K. Dunstan, and M. Rouget. 2013. Fathom Out: Biogeographical Subdivision across the Western Australian Continental Margin - a Multispecies Modelling Approach. *Diversity and Distributions* **19**:1506-1517.

Woolley, S. N. C., D. P. Tittensor, P. K. Dunstan, G. Guillera-Arroita, J. J. Lahoz-Monfort, B. A. Wintle, B. Worm, and T. D. O'Hara. 2016. Deep-Sea Diversity Patterns Are Shaped by Energy Availability. *Nature* 10.1038/nature17937: 10.1038/nature17937.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science* **314**:787-790.

Young, M., D. Ierodiaconou, and T. Womersley. 2015. Forests of the Sea: Predictive Habitat Modelling to Assess the Abundance of Canopy Forming Kelp Forests on Temperate Reefs. *Remote Sensing of Environment* **170**:178-187.

Young, N., B. Legresy, R. Coleman, and R. Massom. 2010. Mertz Glacier Tongue Unhinged by Giant Iceberg. *Australian Antarctic Magazine* **18**:19.